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Povedenie i bioakustika lastonogikh v estestvennoi srede

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Academy of Sciences of the USSR
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Behaviour and bioacoustics of pinnipeds in the natural environment

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In this monograph are presented new and original data on the behaviour and bioacoustics of true seals: the spotted seal [1], the bearded seal and the ringed seal [2], as well as an analytical review of the Soviet and foreign literature devoted to the problem of the behaviour of pinnipeds; consideration is also given to questions relating to the methodology for carrying out ethological and acoustic studies. The monograph is of interest to a wide range of biologists, bioecologists, zoologists, ethologists and bioacousticians.

Editor-in-chief V. M. Bel'kovich

In this monograph are presented the results of original ethological and acoustic studies in the natural habitats of three species of true seals (the bearded seal and the ringed seal in White Sea, and the spotted seal in the waters off Kamchatka and in the Amur liman), as well as a review of the sound signalization of pinnipeds. A classification and description are given of the frequency-temporal characteristics of the main classes of acoustic signals of these species. A methodology is proposed for estimating the population numbers of pinnipeds living under the ice during the reproductive period. A relationship has been revealed between the distribution of the bearded and ringed seals and the different forms of ice formation in the fast ice. An analysis was carried out on the influence of several factors (flow and ebb tide, day and night, anthropogenic effects) on the behaviour and the acoustic activity of the spotted seal, and the role of sound signals in the organization of its social and searching and hunting behaviour has been demonstrated. The ethological and acoustical characteristics of the studied species are considered from the comparative aspect and, on the basis of this, a proposal has been made concerning factors in the evolution of the social behaviour of the true seals.

With 2 illustrations, 37 tables and a bibliography with 321 entries.

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[1] The Russian term "larga" is often used for the common or harbour seal, *Phoca vitulina* L. but it is clear that the authors are treating it as a separate species (*Phoca largha* Pallas, 1811) (page 9 of original text - page 12 of translation) and it is therefore translated here as "spotted seal". [Tr.]

[2] "morskoi zayats" - bearded seal, *Erignathus barbatus* Erxleben; "kol'chataya nerpa" - ringed seal, *Phoca hispida* Schreber. [Tr.]

PREFACE

The pinnipeds may rightly be included among the species that have attracted the attention of scientists for a long time; some features of their morphology, geographical distribution, population numbers, feeding, systematics and physiology have been presented in a large number of publications. Until recent times the majority of the species of pinnipeds were hunted, and some species are even hunted at the present time. Considerable attention has also been paid to determining the stocks, the rates of maturation and reproduction, etc. As a whole, it may be considered that the pinnipeds have nevertheless been studied somewhat incompletely, as their behaviour, distribution and feeding outside of the hunting season, the social structure of their populations, their underwater acoustic signalization and also many other questions require attention.

The Laboratory of Marine Bioacoustics of the P. P. Shirshov Institute of Oceanology of the USSR Academy of Sciences initiated studies on the acoustic signalization and behaviour of pinnipeds in the eighties, in parallel with the studies on the behaviour and the acoustics of the beluga in its natural habitat (Bel'kovich V. M. and Shchekotov M. N. "Beluga. Behaviour and acoustics." Moscow, 1990). Of special interest to us was the hunting behaviour of the pinnipeds in the "river–sea" system, which was studied for several years on the western shore of the Kamchatka peninsula in the Ozernaya, Opala, Golygina and Bol'shaya river, and also in the estuary of the Amur river. The data on the visual and underwater observations on the behaviour were synchronized with the tape recordings of the underwater acoustic signals, and these data were treated in the same way as had been done by us with regard to the Black Sea bottlenose dolphins (Bel'kovich V. M., 1977) and belugas (Bel'kovich V. M., 1987). These data allowed us to show up certain details in the hunting behaviour of the pinnipeds: above all — the highly adaptive nature of the behaviour to changing conditions (weather, species of prey, the rising and ebbing tide, river–estuary–sea, day and night, etc.), including also the anthropogenic conditions (presence, commercial activity, the putting-down and removal of nets, shipping, frightening-away by throwing stones or by gunfire). It was found that the water areas are subdivided into hunting sections, which are not of equal value as to their catch potential, and for this reason the social status of the individual plays an important role in the hunting behaviour. For example, with the incoming tide the seals move into the river and the Alpha individuals are the first to occupy the key positions for hunting and, having caught a fish, they give up their place to the Beta individuals, which are lying in wait from the side or from behind, and so on. It is true that the Alpha may miss the mark, and the fish may fall into the jaws of the Beta or Gamma, which occurrence not always remains unpunished, although during the clarification of the relationships a third seal sometimes gets the fish.

It goes without saying that the behaviour also changes in relation to the numbers of fish. The hierarchical type of behaviour is manifested after the main part of the run and is absent during the latter, but the main part of a run comprises only a two-week episode in a year.

In cases of a pronounced anthropogenic effect only the underwater observations have shed light on the true picture of the hunting behaviour of the seals, since the latter try to keep themselves at a safe distance on the surface and only after diving do they direct themselves towards the feeding places. However, even visual observations above the water surface show a definite pattern in the organization of the hunt: an affinity of the large adult animals to the places where fish were most frequently caught, a gradual floating away of the individuals into the sea as they become sated, i.e. in practice a large part of the micropopulation of a given river passes through the section with the best catch potential during the flood tide - beginning of ebb tide cycle, although more rarely the fish are also caught higher upstream, where the seals, as it were, form a weir ("staggered order"). In this same fashion (in a staggered order) they range themselves also in the sea along the coast, along the migration pathway of a run of fish towards the spawning rivers.

The acoustic signals of the spotted seal are not distinguished by a particular diversity and they have a pulsed character. They are widely used, however, in the organization of the underwater behaviour (designation of location, warning, threat, signal of attack) and are apparently extremely important for orientation, especially in turbid water and during the night hours, which is well correlated with the increase in the numbers of acoustic signals per unit time under these conditions.

Already having a good knowledge of the signals of pinnipeds, we undertook studies during the under-ice (spring) period of their life in the White Sea. The acoustical studies showed that the maximum of the signals clearly coincided with places that were suitable for the setting-up of a lair by ringed seals. Furthermore, contrary to the notion that has taken root in the literature over the last few decades, our studies have shown that in these same places there are also found bearded seals, which are even more active and their signals are especially loud during this spring period of their life, which may evidently be associated with guarding a territory or calling a partner. Thus, the use of acoustic methods has allowed us to shed light on an important feature of the biology of this species. The method developed for counting the population numbers on this basis may play an important role in the organization of nature conservation measures: the estimation and determination of the population numbers, the optimization of the effect of human activity in these natural regions, or its prohibition, etc.

It should be noted that in conducting these studies we obtained considerable support and practical assistance from: the management of the Institute of Oceanology of the USSR Academy of Sciences—Professor V. S. Yastrebov and Corresponding Member of the USSR Academy of Sciences M. E. Vinogradov, the management of SevPINRO [Severnyi Polyarnyi nauchno-issledovatel'skii institut morskogo rybnogo khozyaistva i okeanografii – Northern Polar Scientific Research Institute of Marine Fisheries and Oceanography] (Arkhangel'sk)—Director N. A. Chuksina (Candidate of Biological Sciences), Laboratory Chief V. A. Potelov (Candidate of Biological Sciences) and Yu. K. Timoshenko, the management of KoTINRO [Kamchatskoe otdelenie Tikhookeanskogo nauchno-issledovatel'skogo instituta rybnogo khozyaistva i okeanografii – Kamchatka Branch of the Pacific Ocean Scientific Research Institute of Fisheries and Oceanography] (Petropavlovsk-Kamchatskii) and the management of RKZ (rybokonservnyi zavod – fish cannery) No. 55 in Ozernaya village; in the analysis of the data — IEMEZh AN SSSR [Institut évolyutsionnoi morfologii i ékologii zhivotnykh imenii A. N. Severtsova – The A. N. Severtsov Institute of Animal Ecology and Evolutionary Morphology of the Academy of Sciences of the USSR] —E. V. Romanenko (Doctor of Biological Sciences) and V. I. Markov, and the Acoustic Institute—Professor N. A. Dubrovskii (Doctor of Physical and Mathematical Sciences), and, by way of their critical comments, from Professor V. A. Zemskii (IEMEZh AN SSSR) and Professor A. I. Konstantinov (Leningrad State University). The staff of the Laboratory of Marine Bioacoustics played a key role in obtaining the data and in the creation of this book. A. V. Agafonov and G. A. Boiko (Candidate of Biological Sciences) played a large role in the preparation of the illustrations.

We express our sincere gratitude to all of the mentioned persons and organizations.

Doctor of Biological Sciences V. Bel'kovich

Chapter 1. A brief review of the acoustic signalization of pinnipeds

The systematic study of the underwater acoustic activity of pinnipeds commenced with the work of T. C. Poulter (1963), W. E. Schevill et al. (1963), B. Møhl (1964) and others, although for a long time previously investigators had paid attention to the diversity of sounds that are produced by the polygamous species on their on-shore hauling-out grounds. Over the last twenty years very interesting and diverse data have been obtained on the acoustic signalization of these animals in air, which have allowed us to obtain a picture that possesses a certain integrity. Considerably less is known about the underwater signalization of seals, which is associated above all with the objective difficulties in obtaining the ethological and acoustic data in the natural conditions of the habitat.

The aim of the present review is to examine the data on the underwater acoustic activity of pinnipeds, and in this case it should be noted that, in order to understand the functional purpose of sound signalization of pinnipeds as a whole, it is necessary to consider also the characteristics of the acoustic activity of these marine mammals in the air medium. This necessity is associated with the fact that many of the studied species produce similar sound signals in the air and under water (Californian sea lion, spotted seal, Atlantic grey seal, common seal — Schusterman R. J. et al., 1970), and that in some of the species the signals are distributed and fulfill their function simultaneously in water and in air, if the body of the animal is half submerged in water.

1. Underwater sound signalization

a. Family of eared seals (Otariidae Gill, 1866)

Genus of Californian sea lions (*Zalophus* Gill, 1866).

Californian sea lion (*Zalophus californianus* Lesson, 1828).

The study of the sounds of this species commenced with the work of Poulter (T. C. Poulter, 1963, 1964; H. N. Shaver and T. C. Poulter, 1967). He was able to record a series of pulsed signals produced by the Californian sea lion during the search for fish. The first pulses of the series had a frequency of 3–4 kHz, the frequency of the following pulses increased to 8 kHz and then gradually decreased to 3 kHz. There were also recorded some doublet pulsed signals, and in this case the frequency of the first pulse comprised 4.5–13.4 kHz, while the frequency of the second pulse was always smaller and comprised 2–11 kHz.

Similar series of pulses have also been recorded by other investigators (Schusterman R. J. et al., 1967). Most of these had a duration of about 2 s and less, some lasted for up to 23 s, with pauses of up to 0.5 s. The repetition rate of pulses in a series varied from 5 to 70–80 pulses per second. The major part of the energy in these pulses falls within the frequency 0.8–1.8 kHz. Besides the pulsed series in these experiments, there were noted barking, whinnying, buzzing and sharp cracks [3].

The barking sounds of the males differed only slightly in duration (200–300 ms) and had a frequency of up to 8 kHz. Signals of this type frequently preceded the series of pulses. The females also produce barking sounds in the water and in air (P. Bonnot, 1951).

The duration of the "whinnying" signals was up to 0.4 s, fundamental frequency up to 1.3 kHz, maximal frequency up to 4 kHz. The signals were produced by a 3.5-year old male during aggressive encounters with other individuals.

Series of pulses with a high rate of repetition (buzzing) had a frequency of up to 4 kHz. Fundamental frequency 0.5–1.2 kHz. Duration of series 0.25–0.3 s.

The "sharp crack" is a broad-band pulse with a duration of 0.33 s, which was frequently emitted during rapid swimming. Maximal frequency up to 8 kHz, fundamental frequency up to 2.5 kHz.

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[3] The Russian word "udar" (literally - blow, stroke) is translated here as "sharp crack". Both "bang" and "sharp crack" were used by Schusterman. [Tr.]

Genus of Southern fur seals (*Arctocephalus* E. Geoffroy et F. Cuvier, 1826).
Guadalupe fur seal (*Arctocephalus townsendi* Merriam, 1897).

The sounds were first recorded in 1971 (K. S. Norris and W. A. Watkins, 1971). Low-frequency pulses (150–200 Hz) with a duration of 0.05–0.11 s were produced in series with a repetition rate of a little less than 3 pulses per second. The series were made up of 17–43 pulses, and in this case the frequency of the pulses at the end of the series decreased to 120 Hz. Over the course of an individual pulse a drop in frequency of 5–50 Hz was found. Some of these had harmonic components, the presence of which was not always associated with the intensity of the pulses; it happened that pulses with a low level of intensity had harmonics, while those with a higher intensity level did not have harmonics. In the opinion of the authors this may indicate: 1) some control over the production of harmonics; 2) the presence of individual acoustic characteristics; 3) that harmonics are the result of interference. Two types of pulsed signals were distinguished: 1) with an amplitude that increases over the course of the entire signal or in its terminal part; 2) with a maximal amplitude in its middle part.

The underwater acoustic signals of other species of fur seals have not been studied (I. Stirling and J.-P. Roux, 1987).

Genus of northern sea lions (*Eumetopias* Gill, 1866).
Steller's sea lion (*Eumetopias jubatus* Schreber, 1776).

In spite of the fact that Steller's sea lion produces many roaring and hissing sounds in air, associated with the threatening and territorial behaviour of the adult males during the reproductive season (R. T. Orr and T. C. Poulter, 1967; R. L. Gentry, 1968), the sounds under the water are represented by series of low frequency pulses (up to 2 kHz) with a pulse repetition rate of 20–30 pulses per second (R. J. Schusterman et al., 1970).

b. Family of walruses (Odobenidae J. Allen, 1860)

Genus of walruses (*Odobenus* Brisson, 1762).

Walrus (*Odobenus rosmarus* Linnaeus, 1758).

The sounds which were recorded from an Atlantic walrus held in captivity included vigorous bell-like sounds (frequency 0.4–1.2 kHz) with a duration of 1–1.5 s. The production of such signals is associated with the functioning of the pharyngeal pouches (F. N. Fay, 1960). Besides this there have also been recorded 2 other acoustic signals: 1) rasping; 2) a series of clicks (W. E. Schevill et al., 1966). The rasp commenced with 4–10 pulses with a fundamental frequency of 400–600 Hz, and each with a duration of 0.1 s. If the signal continued then the intensity and the repetition rate of the pulses increased: an almost uninterrupted sound with a fundamental frequency of 200–300 Hz was obtained. The duration of such a signal was 1–2 s. The clicks, with a duration of 0.015–0.02 s and a fundamental frequency of 400 Hz could become joined-up together into a series with a repetition rate of up to 10 pulses per second.

A study of the acoustic signals of walruses in natural conditions permitted the demonstration of 3 principal types of succession of the sounds: 1) a double pulsed signal (frequency of pulses up to 4 kHZ), it precedes the vigorous bell-like sound (0.4–1.2 kHz); 2) a series of pulses which terminates with seven vigorous pulses; 3) a final series of pulses, which commences with three pulses and terminates with a strong pulse, after which the animal rises to the surface (C. Ray and W. A. Watkins, 1975). The pulsed signals have a frequency of up to 4 kHz. The stereotypical and repeated successions of sounds are produced principally at the height of the reproductive season and play an important role in the courting behaviour and, possibly, in individual recognition and the maintenance of underwater territories (J. Stirling et al., 1987).

c. Family of true seals (Phocidae Brooker, 1828)

Genus of hair seals (*Phoca* Linnaeus, 1758).

Common seal (*Phoca vitulina* Linnaeus, 1758).

There are few data on the acoustic activity of this species. The underwater sounds of the common seal, recorded in the same holding tank with a Californian sea lion and Steller's sea lion, had a pulsed character with a predominance of low frequencies (major part of energy up to 1 kHz — R. J. Schusterman et al., 1970). The repetition rate of the pulses in the series varied considerably. It was noted that the acoustic signals were used for purposes of aggressive behaviour.

In a later study (D. Renouf and M. B. Davis, 1982) a report is given about two types of acoustic signals of this species, which were recorded in the natural habitat. The first, which consists of short pulses, with a principal energy of up to 7.5 kHz, may be produced singly or in pairs. The second type of signal consisted of series of impulses, produced with a varying repetition rate. In this and in an earlier study (D. Renouf et al., 1980) the authors noted an increase in the acoustic activity of the common seal during the night hours. While carrying out an experiment under captive conditions they were able to obtain several interesting results: 1) the common seal found a plastic ring in complete darkness; 2) the animal could select the required ring from two that were identical in their superficial appearance but differed in their acoustic properties; 3) the seal emitted single and double pulses while carrying out both types of task; 4) when both rings had the same acoustic properties the animal was not able to distinguish the rings, in spite of the fact that it emitted pulsed signals in this case (D. Renouf and M. B. Davis, 1982). These results appear convincing, despite the subsequent criticism (D. Wartzok et al., 1984).

The study of the signals of the young of the common seal showed that these sounds play an important role in maintaining contact with the mother (D, Renouf, 1984; E. A. Perry and D. Renouf, 1988). The signals were made up of three separate sounds, with a fundamental frequency of up to 3.8 kHz and 4–7 harmonics.

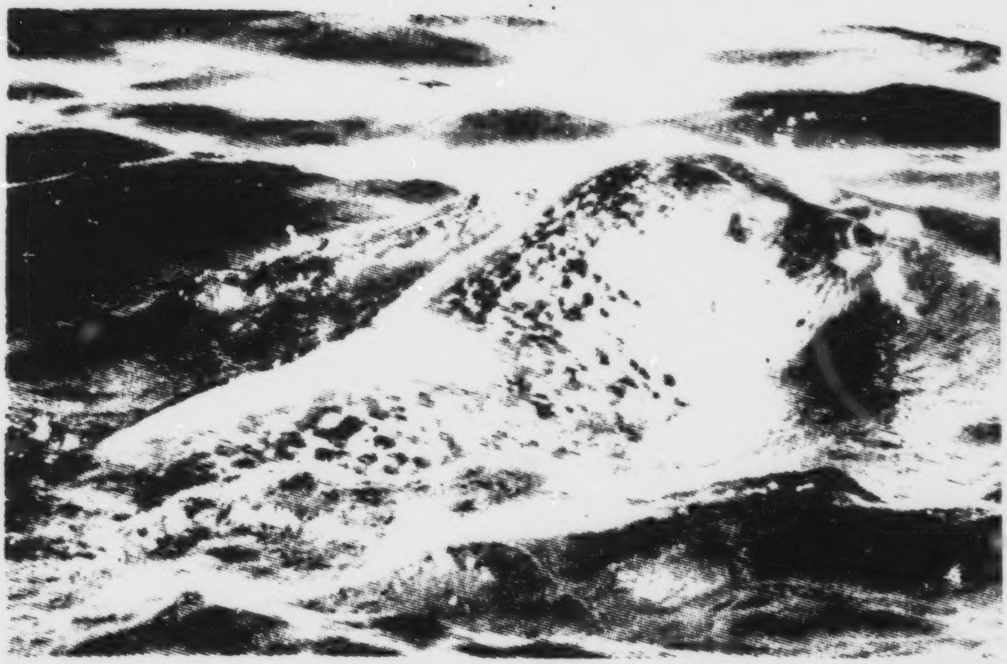

Рис.I. Ларга - вид настоящих тюленей, обычный для тихоокеанского побережья СССР

Figure 1. The spotted seal — a species of true seal (Phocidae), common to the Pacific coast of the USSR.

Spotted seal (*Phoca largha* Pallas, 1811)

The spotted seal is a widely distributed species on the Pacific coast of the USSR (Figure 1). Studies conducted under oceanarium conditions have demonstrated the important role of the underwater vocalizations of the spotted seal during courting and mating (J. C. Beier and D. Wartzok, 1979). In that study a short description was presented of the main classes of acoustic signals: growl, with a duration of 0.02–0.3 s and a fundamental frequency of 0.5 -2.0 kHz; a series of pulses (1-16), following with intervals of 0.08-0.09 s, with a pulse duration of 0.025 s and with the major portion of the energy in the frequency band of 0.5–3.5 kHz; chirp, with a duration of 0.3 s and a frequency of 1.1 kHz; barking,

— 0.075 s and a fundamental frequency of 1.3 kHz; squeak — a signal made up of segments of a pure tone with a duration of 0.02 s and with the major part of the energy within the limits of 2.1–2.8 kHz. It was noted that in the male the predominant signals were "growling" (58.5%) and "series of pulses" (20.4%), while in the female these were "barking" (68.3%) and "series of pulses" (16.1%). Especially many sounds were emitted during the pre- and post-copulatory behaviour.

Genus of ringed seals (*Pusa* Scopoli, 1777).

Ringed seal (*Pusa hispida* Schreber, 1775).

In captivity pulsed signals, often doubled, with a frequency of up to 4 kHz and with intervals of from 2 to 20 ms between the signals, have been noted The pulses had different fundamental frequencies (W. E. Schevill et al., 1963). Studies on the acoustic activity of the ringed seal under natural conditions have revealed the following four types of sound signals: 1) barking — a signal used to express a threat in the course of aggressive interrelationships. The duration of the individual sound is 0.2–0.3 s, with a fundamental frequency up to 1.2 kHz and a maximal frequency up to 3.0 kHz; 2) squealing, apparently associated with subordinate behaviour, with a duration of 0.2 s; the major portion of the energy of the signal fell in the range of pulses with frequencies of 1.0–1.2 kHz and 2.5–3.0 kHz; 3) growling — a signal that is possibly also utilized for expressing a threat, with a duration of up to 0.5 s and a fundamental frequency of up to 2.0 kHz. Maximal frequency up to 6.5 kHz; 4) chirping — a signal with a duration of 0.2–0.3 s and with a fundamental frequency that decreases gradually from 2.0 kHz to 1.8 kHz (J. Stirling, 1973).

Genus of harp seals (*Pagophilus* Gray, 1844).

Harp seal (*Pagophilus groenlandica* Erx., 1777).

A comparatively large diversity of underwater sounds, which are apparently utilized for purposes of communication, have been noted in this species (Møhl B. et al., 1975). The latter investigators distinguished fifteen kinds of signal: 1) "sinusoid" — with a duration of up to several seconds, maximal frequency up to 2 kHz; 2) "whistle" — distinguished from the first by its greater frequency (3–5 kHz) and a small drop in frequency at the beginning of the signal; 3) "Morse code" — a sinusoidal wave with a frequency of 0.5 kHz, produced in two sections, each of 100 ms; 4) "trill" – with a duration of about 1 s, it is characterized by a frequency modulation of the carrier frequency (2–5 kHz) (modulation frequency about 28 Hz); 5) "gull's cry" — this signal commences with a frequency of 1–2 kHz and then drops to 0.8 kHz; each of these segments has a duration of 0.2–0.3 s; 6) "chirp" — a high-frequency signal (up to 10 kHz) with a duration of about 0.15 s, the frequency of which drops from the initial 6 kHz to 4.5 kHz and then increases once more. The signals usually follow in pairs, with intervals of 0.6 s; 7) "complex trill" — a combined signal of pulsed and frequency-modulated structures with a fundamental frequency below 1 kHz (modulation frequency about 30 Hz) and a duration of 0.4–0.5 s; 8) "dove's cooing" — made up of segments with a duration of 50 ms, which join up together at the end of the signal; 9) "signal with displaced frequency" — composed of 10 components, each of which continues for 0.2 s; over the course of the first 75 ms the complex harmonic structure of each component has a fundamental frequency of 0.93 kHz, after which there occurs a sharp drop in frequency (in 20 ms) to 0.6–0.7 kHz, which is preserved over the final 100 ms; 10) "cry of thrush" — produced in the form of a sequence of signals, similar to the first 75 ms segment of the signal of the previous class; 11) "twittering" — a signal with a rapidly changing frequency of up to 1.6 kHz; 12) "tiok"[4] — this signal commences

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[4] "tiok" is a transliteration of the Russian "ТЬЯОК" ("t'iok") - probably an onomatopoeic neologism. [Tr.]

with a frequency of 1 kHz and then, after 50 ms, drops to 0.5 kHz. Most frequently encountered are sequences of 4 signals; 13) "squeal" — this has a fundamental frequency of up to 0.6 kHz, a maximal frequency of up to 2.2 kHz and is made up of a certain number of pulses with a duration of 10 ms. This signal is apparently utilized in intraspecific aggressive interrelationships; 14) "grunt" — the most common signal. Usually made up of two identical segments, composed of pulses (1--2 ms), the carrier frequency of which is about 2 kHz, and having harmonic components. The duration of each segment is 120–200 ms; 15) "sharp cracks" — series of 4 pulses, the duration of each of which comprised 40 ms, while the duration of the interval between the pulses was 0.2 s. Major part of the energy of the signals up to 6 kHz.

Furthermore, when the speed of transport of the magnetic tape was slowed down by a factor of 8, there were revealed some intensive single clicks, with a duration of 100–200 nanoseconds, the maximal energy of which occurred at a frequency of 32 kHz.

Observations on the harp seal in the natural habitat indicate that the underwater vocalizations of this seal are a necessary component of the threatening displays and are accompanied by streams of air bubbles emerging from the nostrils of the animal (B. R. Merdsoy et al., 1978).

The application of automatic recording of the underwater sound signals of the harp seal has made it possible to establish that the usual frequency of the signals produced comprises 32–88 per minute (J. M. Terhune et al., 1987). In the sequences of signals there have been noted such that are sounded several times and are repeated, on average, 1.9–4.7 times in one sequence. About 30% of the signals are not repeated even once.

Genus of grey seals (*Halichoerus* Nilsson, 1820).

Atlantic grey seal (*Halichoerus grypus* Fabricius, 1791).

Recordings have been made in a holding tank of pulsed signals with a frequency of up to 12 kHz, often proceeding in pairs, with intervals of 0.01–0.02 s between the pulses, and sometimes in series with a repetition rate of 70–80 pulses per second (R. J. Schusterman et al., 1970). Individual components of the signals had a frequency of up to 30 kHz. The average duration of the 12 recorded "buzzes" comprised 2.1 s, maximal frequency up to 1.3 kHz. In the course of the observations it was noted that the acoustic signals were produced only during social contacts (pursuits, contacts with one another, etc.). The authors propose that these sounds play a key role in the communication system of these animals.

Genus of bearded seals (*Erignathus* Gill, 1820.

Bearded seal (*Erignathus barbatus* Erxleben, 1777).

Only one study has been devoted to the sounds of the Pacific subspecies of the bearded seal — the "lakhtak"[5] (C. Ray et al., 1969). It was shown that the acoustic signals, which comprise protracted, melodious, frequency-modulated trills, with a duration of about 1 minute, were produced by mature males during the reproductive season. In the signal there was observed a directed drop in the frequency approximately from 2–3 kHz to 200 Hz, in spite of the temporary short increases in the frequency. 15 s after the termination of the trill a non-modulated, low-frequency moan, with a duration of 2–3 s was quite often emitted. In the opinion of the authors, these signals are used for purposes of territorial and reproductive behaviour.

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[5] "Lakhtak" is a transliteration of the Russian term for the Pacific subspecies of *E. barbatus* Erx. [Tr.]

Genus of crab-eater seals (*Lobodon* Gray, 1844).

Crab-eater seal (*Lobodon carcinophagus* Hombron et Jacquinot., 1842).

The crab-eater seal produced sounds that resemble a moan, with a mean duration of 2.2 s. The major part of the energy fell in the frequency region up to 1.5 kHz. Maximal frequency above 8 kHz (J. Stirling and D. B. Siniff, 1979).

Genus of leopard seals (*Hydrurga* Gistel, 1848).

Leopard seal (*Hydrurga leptonix* Blainville, 1820).

Recordings have been made with the leopard seal of series of short pulses which follow at a rapid rate and fuse together into an almost uninterrupted signal. Each series was made up of two parts. The number of pulses in a series was greater than 450. The frequency of the overwhelming majority of the pulsed signals did not exceed 5.9 kHz (J. Stirling and D. B. Siniff, 1979). At least some of them are associated with reproductive behaviour (B. J. Marlow, 1967).

Series of ultrasonic pulses were produced by the leopard seal when live fish were released into the holding tank with the animal. The major part of the energy of the pulses, with a duration of 4–10 ms, usually fell into the frequency zone of 50–60 kHz, with some individual spectral components attaining a frequency of 164 kHz (J. A. Thomas et al., 1982).

Genus of Weddell's seals (*Leptonychotes* Gill, 1872).

Weddell's seal (*Leptonychotes weddelli* Lesson., 1826).

Weddell's seal (Figure 2A) produces the most unusual sounds among the pinnipeds (W. E. Schevill and W. A. Watkins, 1965; C. Ray, 1967). A series of pulsed signals (1–10 kHz, usually 1–2 kHz) proceeds initially at a high rate (up to 140 pulses per second) and then the repetition rate gradually decreases, and at the same time the spectral frequency of the pulses also decreases. The duration of such a series ranged up to 42 s. The intensity of the pulses is frequently 40 dB higher than the surrounding background noise; they may have 2-3 components with a successively decreasing frequency; the pulses in series with a high repetition rate are apparently composed of a single component. The duration of individual pulses varies from 0.005 to 1.5 s. It was noted that interrupted trills, puffing and low-frequency sounds are utilized by the males while courting the female (C. Ray and M. A. De Camp, 1969). Later studies demonstrated a directionality of the sound beam (W. E. Schevill and W. A. Watkins, 1971).

In the course of a study of the behaviour and underwater vocalizations of Weddell's seal in the natural conditions of the habitat (G. W. Kaufman et al., 1975), with the use of television cameras, it was noted that series of pulsed signals were produced by the males during aggressive encounters, and in this case the authors have proposed that the setting up and maintenance of the underwater territorial borders proceeds mainly with the aid of acoustic signalization. Other investigators have noticed a large repertoire of underwater acoustic signals of this species of seal (12 types with 34 classes), from short pulses to protracted frequency-modulated signals, with a frequency of up to 15 kHz (J. Thomas et al., 1983). Individual vocalizations were played in the immediate vicinity of reproducing colonies. Specific responses were obtained to the signals presented. In the opinion of the authors, most of the signals are utilized for purposes of reproductive behaviour (protection of territories, aggressive-submissive behaviour). One of such types of signals, produced during pupping, was the "song", made up of six structural elements, with a total duration of up to 1 minute, the dominant frequency of which comprised 0.5–4 kHz (K. Green and H. R. Burton, 1988).

An attempt was made to study the underwater acoustic activity of Weddell's seal by means of automatic recording: the tape recorder was switched on for 2.5 minutes over certain intervals of time (G. A. Thomas et al., 1988). The recordings were carried out over the course of several years during the reproductive season. As the principal classes of signals, the authors distinguished trills, puffing, twittering, cricket cries, bangs and the

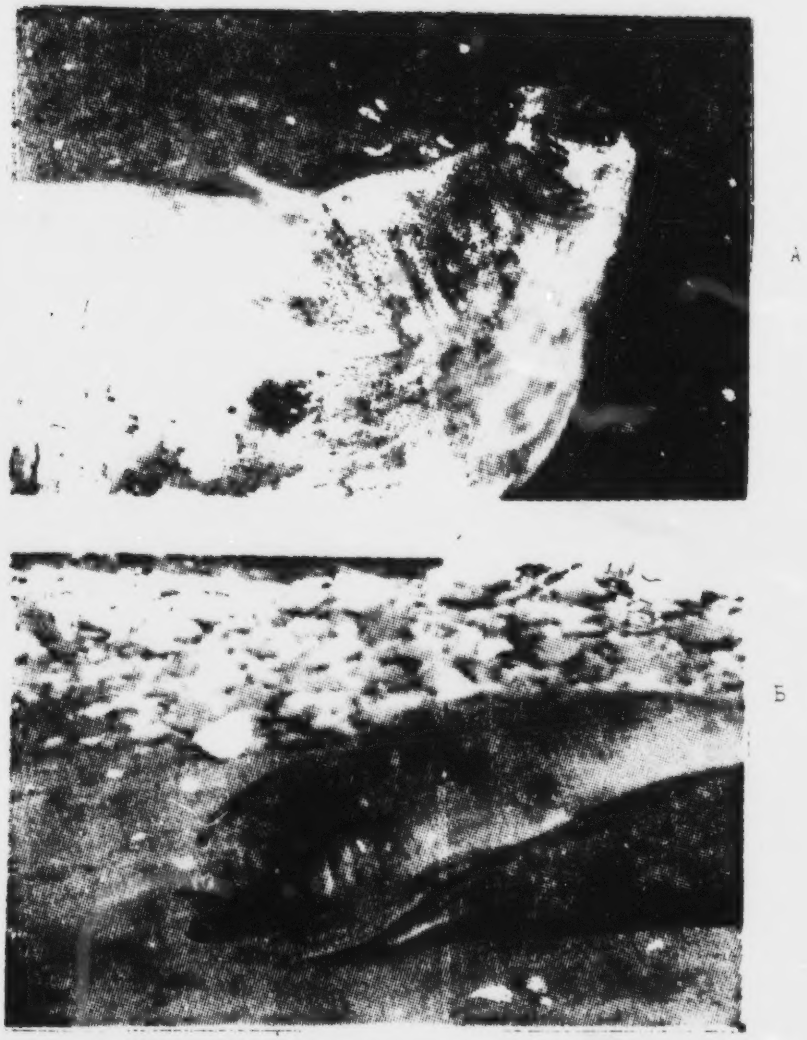

Рис.2. Тюлени Южного полушария: А – тюлень Уэдделла;
Б – южный морской слон

Figure 2. Seals of the Southern hemisphere: A - Weddell's seal;
Б - Southern elephant seal.

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signals of the young animals. On the basis of the results of an analysis, the peak of signalization falls into the mating period. The signals of the young animals, however, are most frequently recorded at the time of the discontinuation of the milk feeding. The frequency of occurrence of the first three classes of signals depended on how many females with young were present on the ice.

Studies carried out in two remote sections of the distribution range of the Weddell seal have shown that the repertoire of the underwater sounds in these seals differs (J. Thomas and J. Stirling, 1983). The classes of signals that were noted in the two regions differed only slightly in their frequency and temporal characteristics, but there were also noted vocalizations that were specific to each of the regions. In the opinion of the authors, these differences are associated with the strong attachment to the sites of reproduction, polygamy and learning.

Genus of hooded seals (*Cystophora* Nilsson, 1820).

Hooded seal (*Cystophora cristata* Erxleben., 1777).

In captivity the hooded seal produced clicks in a broad band from 0.1 to 16 kHz, with various fundamental frequencies (W. E. Schevill et al., 1963).

It has been established by other investigators that males of the hooded seal may produce 3 types of underwater sounds: 1) growls, with a duration of 0.5–1 s and a fundamental frequency of 0.2–0.4 kHz; 2) snorting, with a fundamental frequency of 0.1–1.0 kHz and individual harmonics up to 3.0 kHz; 3) high-frequency buzzing, with a fundamental frequency up to 1.2 kHz and a maximal frequency up to 6.0 kHz (J. M. Terhune and K. Ronald, 1973).

2. Acoustic signalization of pinnipeds in air

The polygamous species of pinnipeds, which form dense groups on the hauling-out grounds during the reproductive period, with a complex structure of the population on the hauling-out grounds, make use of various acoustic signals in their interrelationships with one another.

In considering the diverse behavioural elements of the pinnipeds, one may distinguish four basic types of social interactions of the animals: 1) territorial and aggressive behaviour — of the adult males, and of the females with young; 2) sexual behaviour; 3) interrelationships of the females and the young animals; 4) play behaviour of the young animals. The airborne acoustic signals may be classified in association with these principal types of behaviour.

a. Sound signals of pinnipeds, associated with territorial and aggressive behaviour

Northern fur seals make use of two types of signals, belonging to this group. When a new male appears on the hauling-out grounds, the territorial bulls with harems, that are closest to it, become alerted. On noticing the movement of a stranger close to its territory (at a distance of 12–15 m) the harem bull raises up high the anterior part of its body ("vertical" threatening posture - P. Paulian, 1964), looks in the direction of his rival and emits a warning booming bellow, opening wide his mouth and shaking his head. The duration of an individual signal is 1.2–1.6 s, and its fundamental frequency lies within the range of 400–500 Hz (T. Yu. Lisitsyna, 1973). The signal is modulated in amplitude, which is a widely utilized measure for increasing the noise immunity of the signal in mammals (A. A. Nikol'skii, 1973).

When a stranger or a neighbouring territorial bull approaches the borders of the section, the male immediately assumes a threatening posture, at the same time emitting a series of jerky coughing sounds—the threatening cough. This signal is made up of 3–5 sounds with a duration of 0.06–0.13 s. The energy maximum of the frequency spectrum of the signal lies in the region from several tens to 500 Hz. Less intensive frequency components extend up to 4 kHz (T. Yu. Lisitsyna, 1981). The threatening cough is a sound signal with a close range action; it has an interrupted character (A. I. Konstantinov et al., 1978).

In the defense of their borders the adult males of the southern fur seal (*Arctocephalus townsendi*) also make use of threatening coughs that are similar to the coughing of the northern fur seal (G. A. Bartholomew, 1953; R. S. Peterson et al., 1968). Another territorial signal is barking. The duration of an individual sound is about 0.25 s. The major part of the energy falls in the 2-3 kHz frequency range, although some individual harmonics attain a frequency of 7-8 kHz (R. S. Peterson et al., 1968).

The males of the Guadalupe fur seal produce a multitude of sounds during the reproductive season and their vocalizations are a constituent part of the aggressive behaviour of the males (M. O. Pierson, 1987). The author distinguishes 4 classes of signals: 1) intensive threat signal, with a duration of 1.1–1.8 s, the major part of the energy of the signals in different males attains 1.5–4 kHz; 2) the threatening cough (boundary puff)[6] is a signal that is always emitted with a lunge in the direction of the adversary, it is composed of a series of sharp sounds, the duration of which comprises 0.08–0.12 s, with the major part of the energy lying in the frequency range up to 3–4 kHz; 3) barking - a low-frequency, recurring signal which, depending on the behavioural situation, varies markedly in the frequency of repetition, duration and intensity; the duration of the signals ranged from 0.09 to 0.12 s, dominant frequency up to 2 kHz. Barking is produced during the patrolling of the territories, during interrelationships with females and with other males, and also while maintaining borders; 4) low-frequency growling (growl), also varying in duration and intensity. The frequency and temporal characteristics of this class of signals, which are used in similar situations as the barking, were not presented in the paper.

The males of the Sub Antarctic fur seal (*Arctocephalus tropicalis*) also produce threat signals when they are on their own protected section of the hauling-out grounds (J.-P. Roux and P. Jouventin, 1987). Their duration varied from 0.8 to 1.5 s, while the dominant frequency, as a rule, did not exceed 2 kHz, although some individual frequency components were noted up to 4-5 kHz. The authors especially emphasize the individual character of these signals and the possibility for the individual recognition of the males by one another.

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[6] "threatening cough" is a literal translation of the Russian "угрожающее хорканье"; (boundary puff) [probably Pierson's term] - occurs as such in the original Russian text. [Tr.]

The warning bellow of the territorial male Steller's sea lion also gives notice to potential rivals that a harem section is occupied. The duration of this powerful sound ranges from 0.95 to 3.5 s, while the energy maximum of the fundamental frequency lies in the range of 250–300 Hz (T. Yu. Lisitsyna, 1976; 1979). The bull sea lion neighbours, that are on the borders of their sections, emit another sound signal - threatening huffing. Its function is a threat and a demonstration of the strength of the rivals, frequently anticipating a skirmish. The major part of the energy of the signal is concentrated in the range up to 400 Hz. The duration of the signal is 0.6–0.85 s (T. Yu. Lisitsyna, 1979).

The principal type of acoustic signals of the territorial males of the Californian sea lion are sounds that resemble barking, with a duration of 0.3–0.4 s and a frequency of up to 2.5 kHz. The major part of the energy falls on the harmonics up to 1 kHz (R. S. Peterson and G. A. Bartholomew, 1969). In a specific behavioural situation changes occur in the repetition rate, the loudness and the degree of directionality of the acoustic signals. The repetition rate of the signals and their number increased markedly when females are present on the territory of a given male, when the male is moving and when there are mutual displays on the borders (R. J. Schusterman, 1977). Furthermore, when sea lions were kept in captivity it was found that the dominant male of a group of six animals produced the largest number of sounds. When this animal was transferred into another holding tank, the male that was next in rank began to produce the greatest number of sounds (R. J. Schusterman and R. G. Dawson, 1968). It is of interest that a male which is trespassing on another male's territorial section does not produce any sounds (R. S. Peterson and G. A. Bartholomew, 1967).

During the course of the reproductive season the males of the Galapagos sea lion produce a series of amphibial sounds, resembling barking, when patrolling a particular section of the shore. The number of sound signals in a series comprised 5.5 on average. The series were repeated with an interval of 4.3 s (R. T. Orr, 1967).

In the males of the Northern elephant seal 4 types of vocalization have been distinguished; 3 of these are associated with threatening and territorial behaviour (J. E. Fitch and R. C. Wilson, 1949; G. A. Bartholomew, 1952; F. E. Sandegren, 1976). The most common type of vocalization was represented by series (6–13) of signals, the duration of which comprised 0.3–0.5 s, with a repetition period of 0.4–0.6 s. The energy maximum of the frequency spectrum of the signal is located in the range from 250 to 300 Hz. Less intensive frequency components extend to 2 kHz. It was noted that these signals are also utilized for the individual recognition of the animals (B. J. Le Boeuf, 1971), which assists in decreasing the probability of physical conflicts, and, moreover, these signals possess characteristics that permit one to rapidly establish the location of the animal (P. Marler and W. J. Hamilton, 1966). The presence of dialects is characteristic of the separated island populations of the Northern elephant seal (B. J. Le Boeuf and R. S. Peterson, 1969; B. J. Le Boeuf and L. F. Petrinovich, 1974 a, b). The difference in the airborne acoustic signals of the males of the Northern and the Southern elephant seals (Figure 2B), which diverged millions of years ago, is even more considerable. The sounds associated with the aggressive and territorial behaviour of the Southern elephant seal were irregular in time and lasted, on average, for 19 s. On the other hand, the Northern seals produced regular series of pulsed signals, which rarely lasted for more than 6 s. The average fundamental frequency of the signals for the Southern elephant seals comprised 233 ± 90 Hz, while for the Northern seals this value was 202 ± 54 Hz (B. J. Le Boeuf and L. F. Petrinovich, 1974).

On the whole, in step with the increase in the body dimensions of the pinnipeds with age, the acoustic signals acquire a lower frequency (T. C. Poulter, 1968; M. Caldwell and D. C. Caldwell, 1972), and their intensity and duration also increase (G. A. Bartholomew and N. E. Collias, 1962).

Not much is known about the acoustic activity of the males of the true seals which lead a less social way of life. Weddell's seal utilizes long series of sound signals in its aggressive and territorial behaviour (A. A. Lindsey, 1937; C. Ray, 1965, 1966; C. Ray and M. A. De Camp, 1969).

In their aggressive interrelationships and the protection of their individual and family lairs, the females of the Northern fur seals make use of two types of sound signals. On an encounter with another female, the animal initially produces a threatening snort - a signal with a duration of 0.55 s, with a fundamental frequency of 0.4 kHz, while with increasing tension in the situation it produces a threatening coughing, comprising a series of signals (5) with a duration of 0.06–0.17 s, with a fundamental frequency of 0.6 kHz and an upper range of frequency components of 4.0 kHz (T. Yu. Lisitsyna, 1973).

At a low level of tension in a conflict the females of Steller's sea lion produce a prolonged threatening sound (up to 2,5 s) with a fundamental frequency of 344 Hz or threatening grunting sounds (duration of individual signal 0.45 s, fundamental frequency 400 Hz). Another type of signal, threatening huffing, reflects the highest degree of tension in the situation. Its duration is 0.6 s and its fundamental frequency is 250–300 Hz (T. Yu. Lisitsyna, 1980).

Approximately 90% of the encounters of females of the Northern and the Southern elephant seals are limited to threatening vocalizations (B. J. Le Boeuf et al., 1972; T. E. Christenson and B. J. Le Boeuf, 1978; T. S. McCann, 1980, 1982), and in this case their sound signals have a higher frequency (G. A. Bartholomew and N. E. Collias, 1962), as compared with the signals of the males.

The females of the California sea lion produce the distant threatening signal - barking, more rarely than the males (R. S. Peterson and G. A. Bartholomew, 1967; T. C. Poulter, 1968). Besides this, they may produce three types of vocalization, corresponding to an increasing level of aggressive behaviour: squealing, roaring sounds (with a duration of up to 1 s, with the major part of the energy in the range up to 2 kHz) and growling (major part of energy up to 1.5 kHz, individual components up to 4 kHz, with a duration of more than 2 s) (R. S. Peterson and G. A. Bartholomew, 1969).

On the approach of a man the female of the Hawaiian monk seal, protecting her young, produces a low threatening bellow (D. W. Rice, 1964).

b. Acoustic signals associated with sexual behaviour

The males of the Northern fur seal and of Steller's sea lion produce two types of signals that belong to this group. When it is on its harem territory the bull seal constantly produces a sound which is made up of a series of short pulses, remotely resembling a clatter. In the breeding behaviour the clattering sound, alternating with the harem cry (see below), is accompanied by bowing of the head towards the female and sniffing of the latter. On the whole, however, the male clattering is a signal that marks an active male, i.e. that designates the sex. It is composed of a series of from 2 to 36 pulses with a duration of 0.02–0.04 s, which follow with a period of 0.07–0.16 s (T. Yu. Lisitsyna, 1973). The fundamental frequency of the male clattering lies in the range of 0.8 kHz, accompanied by a well evident harmonic of 1.6 kHz. During his movements close to the females, before and after sniffing, and also between repeated sniffings of the female, the bull seal emits a low short sound, resembling jerky mooing - the harem cry. This signal in combination with the clattering, the sniffing of the female and several characteristic postures, is included in the breeding behaviour complex of the male. The fundamental frequency of the signal lies in a range around 300 Hz and may be accompanied by a frequency component in the range of 800 Hz (T. Yu. Lisitsyna, 1973).

In relation to the bulls the females of the Northern fur seal display a behaviour which uniquely anticipates and relieves aggressive behaviour, but which does not have any special sound signal.

The males of Steller's sea lion most frequently produce a signal resembling a series of grunting sounds, accompanied by nods of the head. T. C. Poulter (1968) calls this the "nodding signal". This little-specialized signal combines the function of the harem cry and the clattering of the Northern fur seals; the bull sea lion accompanies its courting and mating with this signal, and also uses it also to notify the surrounding individuals of the presence of a male. The number of sounds in a series ranges from 1 to 6. The duration of an individual sound is 0.42 s. The fundamental frequency lies in the frequency range up to 250 Hz (T. Yu. Lisitsyna, 1979).

In their breeding behaviour the males of the Californian sea lion make use of acoustic signals that resemble barking, similar to the signals during aggressive and territorial interactions, although the repetition rate and the number of signals in the series varies in this case (R. S. Peterson and G. A. Bartholomew, 1969; R. J. Schusterman, 1977).

c. Sounds utilized in interactions with the young

The females of the polygamous species of pinnipeds, which reproduce in teeming colonies on shore, regularly meet with their young among thousands of other individuals, sometimes after a long absence in the sea. This is all the more amazing, because the young animals move considerable distances over the hauling-out grounds and frequently gather into groups of their own age. The only probable hypothesis which explains this phenomenon is the individual recognition of the animals by means of highly specific acoustic signals, and in the final phase of recognition—by the smell (V. A. Vladimirov, 1975; T. Yu. Lisitsyna, 1972, 1990). It is possible that towards the end of the feeding period the females of the Northern fur seal may often recognize their cubs also purely by visual means (V. A. Vladimirov et al., 1982; V. A. Vladimirov, 1990; K. A. Ono, 1972).

Although there is scarcely any evidence of individual recognition (with the exception of L. F. Petrinovich, 1974, and F. Trillmich, 1981), most authors consider that the females play a more active role in the recognition of their young (R. M. Laws, 1956; G. A. Bartholomew, 1959; J. Stirling, 1970; L. F. Petrinovich, 1974; F. Bruemmer, 1975; A. G. McNab and M. C. Crawley, 1975). Other authors (R. W. Rand, 1967; F. E. Sandegren, 1970) have proposed that the young also participate in the process of recognition of the female. This is apparently of great importance, since the young animals subject themselves to considerable danger by approaching strange and often extremely aggressive females (S. C. Fogden, 1971; B. J. Le Boeuf and K. Briggs, 1977; T. S. McCann, 1987).

Recent studies on the characteristics of the behaviour and sound signalization of the Galapagos for seals and sea lions have demonstrated the existence of a mutual recognition of the mother and the young (F. Trillmich, 1981). The high acoustic activity and intensive interactions of the mother and the young calf immediately after birth apparently serve to establish recognition in the first hours (female) or days (calf). An analysis of the sound signals produced by the females and by the young animals has shown that the diversity of sounds provides the necessary foundation for individual recognition in these species (F. Trillmich, 1981). Mutual recognition of the females and young of the Northern fur seal and of Steller's sea lion only on the basis of acoustic signalization becomes possible when the young attain an age of 1–1.5 months (T. Yu. Lisitsyna, 1981).

In the true seals which form very plentiful colonies on shore, and in particular in the Atlantic grey seal, the females recognize their pups individually (T. G. Smith, 1966; S. C. Fogden, 1971). The mechanism of this recognition is less reliable, however, than in the eared seals or at least it is easily disturbed by anthropogenic influences S. C. Fogden, 1968; T. G. Smith, 1968), possibly as a consequence of more irregular feeding of the young and an inadequate degree of development of the social structure from the time of the last glaciation (J. Stirling, 1975).

The characteristics of the acoustic signalization of the eared seals are very diverse. Returning from feeding, the female of the Northern fur seal produces a prolonged calling cry, resembling bleating, immediately on coming out onto the land and sometimes even from the water. The signals of the females differ from one another in their fundamental frequency, which is distinctly expressed and constant in each individual according to the character of the spectrum and according to the frequency of the amplitude modulation. The duration of the signal is 0.6–1.6 s. The frequency of the amplitude modulation is 30–80 Hz. The fundamental frequency lies within the limits of 0.5–1.0 kHz (T. Yu. Lisitsyna, 1980, 1986). The hungry pup, in its turn, tries to find its mother and moves around the hauling-out grounds repeating its cry, a thin bleating. The duration of this signal varies from 0.55 to 1.77 s. The fundamental frequency of 0.8–1.0 kHz is accompanied by numerous harmonics up to 4 kHz. Pups older than one month are apparently recognized by the females by their voice, which is possibly associated with the modulation in amplitude of the signals of the young animals of this age (T. Yu. Lisitsyna, 1981). The fairly great duration of the calling cries of the Northern fur seal females and of their young (respectively, on average, 1.18 and 1.27 s) is associated with the combined effect of a whole series of factors, hindering an establishment of contact: the noise level on the hauling-out grounds, the aggressive behaviour of the animals on the hauling-out grounds, etc. (T. Yu. Lisitsyna and A. A. Nikol'skii, 1986). On the whole, in both the females and in the young of the Northern fur seal one finds a clearly expressed situational variability of the sound signals (T. Yu. Lisitsyna, 1988).

In the female of the Galapagos fur seal the signal that attracts the young animal is usually made up of two parts. The first half is represented by almost parallel frequency bands with slight differences in amplitude. The second has a considerable degree of amplitude modulation in the frequency ranges of 0.65–0.9 kHz and 1.4–2.0 kHz. The duration of the answering cry of the young animal comprises 0.5–0.8 s, and the major part of the energy of the signal falls on frequencies of 0.5–2.0 kHz, although some individual harmonic components attain values of up to 6.0 kHz (F. Trillmich, 1981).

When contacting its young the female of the Southern fur seal (*Arctocephalus townsendi*) produces sounds with a duration of about 1.5 s, with a fundamental frequency of 1–1.5 kHz and with harmonic components of up to 6–7 kHz (R. S. Peterson et al., 1968).

For attracting their young the females of the Sub Antarctic fur seal (*Arctocephalus tropicalis*) produce signals with a duration of up to 1.8 s, the dominant frequency of which comprises 2-3 kHz (J.-P. Roux and P. Jouventin, 1987). The authors were able to demonstrate the important role of these signals for the mutual recognition of the females and the young. The calling cries of the of the different females have an expressed individual variation. Every young animal also emits calling cries that have a unique aggregate of frequency and temporal characteristics. The signals of the young animals have a higher frequency: the dominant frequency is 4-5 kHz, and their duration is more than 1 s.

In the Kerguelen fur seal (*Arctocephalus gazella*) the females, when calling their young, emit signals that last for about a second, with the major part of their energy falling on frequencies up to 2 kHz (P. D. Shaughnessy and L. Fletcher, 1987), while the young animals produced calling cries with a duration of 0.7–0.8 s and with their dominant frequency extending to 5-6 kHz (I, Stirling and R. M. Warneke, 1971; M. O. Pierson, 1987).

The duration of the calling cry of the female of Steller's sea lion is 1.48 s, while the fundamental frequency of this signal is 500 Hz. Amplitude modulation is found in 30% of the signals of the females, and in this case it is usually the beginning or end of the signal that is modulated. The signals of the pups are somewhat shorter (1.1 s) and of a higher frequency (800 Hz) (T. Yu. Lisitsyna, 1981).

In searching for their young the females of the Galapagos sea lion make use of sound signals with a duration of 0.6–1 s , the major part of their energy falling into the frequency range of 0.3–0.6 kHz and 1.0–1.7 kHz. The fundamental frequency of 0.7–1.5 kHz of the signal of the young animals, with a duration of 0.5–0.9 s, is accompanied by harmonics up to 6.0 kHz (F. Trillmich, 1981).

The calling cry of the females of the Californian sea lion lasts for 1-2 s. The major part of the energy falls in the frequency range of up to 1.8 kHz, with individual harmonic components extending to 5 kHz. The signals have a well expressed frequency modulation and are distinct for each individual. The calling cry of the young animal has characteristics that resemble the calling cry of the female. The duration of the signal is 1.5–2 s, while its fundamental frequency (800 Hz) is accompanied by harmonic components up to 4 kHz (R. S. Peterson and G. A. Bartholomew, 1969).

Not much is known about the sounds used in the contact of the females with their young in the true seals. The calling cry of the female of the Northern elephant seal has a fundamental frequency of 0.8–1 kHz with 4–8 harmonics (G. A. Bartholomew and N. E. Collias, 1962).

The young of the common seal emits a calling cry with a duration of 2-3 s when it is separated from its mother. The major part of the energy of this signal is concentrated in the frequency range of 0.4–0.7 kHz and 0.95–1.2 kHz (W. E. Evans, 1967). The female does not produce an answering cry, but swims up to the young animal and, if after a nasal contact the young animal is deemed to be its own, then it attaches itself to the female. After the young animal changes over to an independent way of life, a signal of this type is no longer produced (W. E. Evans, 1967).

When a starved young animal of the "antur" seal[7] (*Phoca kurilensis*) was held in an open-air cage it regularly emitted calling cries which resembled the crying of a child in arms (A. I. Konstantinov and V. N. Movchan, 1985). The signals had a duration of about 1.5 s and a dominant frequency of 0.3–0.6 kHz; in the opinion of the authors these signals were addressed to the mother.

In spite of the fact that the males of the Galapagos sea lions displayed some care for their young (J. Eibl-Eibesfeldt, 1955; G. W. Barlow, 1972), no special sounds were noted with this behaviour.

d. Acoustic signals associated with the play behaviour of the young animals

On attaining an age of 4–5 weeks the young animals of the eared seals begin to move about more in the absence of their mothers on the hauling-out grounds and not infrequently they gather together in groups. From this time there occurs a development and complication of the play behaviour of the pups, which mainly comprises trial skirmishes and is closely connected with the subsequent formation of the social relationships (O. A.

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[7] "Antur" is the Russian term for *Phoca kurilensis*. [Tr.]

Rasa, 1971; R. Fagen, 1974; R. L. Gentry, 1974). The acoustic repertoire of the young males in this case is supplemented by a new characteristic signal: the combat cry.

The combat cries of the young males of the Northern fur seal may be composed of both a series of short pulses with indefinitely varying pauses, as well as of single sounds of greater duration. The duration of the individual pulses in the series is 0.2–0.7 s, and of the single cries - up to 0.9 s. The signal is modulated in frequency. The fundamental frequency varies within the range of 400–600 Hz (T. Yu. Lisitsyna, 1973). Usually the animal emits a combat sound having suffered a defeat in a trial skirmish.

The duration of the combat cries of the young males of Steller's sea lion is 0.4–0.7 s, with a fundamental frequency of 500–800 Hz. The frequency spectrum includes several distinct, deeply modulated frequency components of up to 1.5–2.0 kHz (T. Yu. Lisitsyna, 1980).

In their play the young animals of the Southern fur seal (*Arctocephalus townsendi*) emit a characteristic barking and guttural sounds, resembling coughing (R. DeLong, 1968; R. S. Peterson et al., 1968).

3. Conclusion. Functional designation of the underwater acoustic signalization of pinnipeds

Before turning to the question of the functions of the underwater sound activity of pinnipeds, it is necessary, in our opinion, to briefly consider certain aspects of the generation and reception of sound signals by pinnipeds, and also to evaluate the degree to which they make use of the visual analyzer for purposes of orientation and searching and hunting behaviour.

Vision of pinnipeds. The vision of these predators, not infrequently used at a great depth (G. L. Kooyman, 1966, 1967) and during the night, is sensitive to very weak light (G. L. Walls, 1942; E. S. Hobson, 1966). Investigations have led to the revelation of several adaptive features of the eyes of pinnipeds, in particular, to the high refractive power of the crystalline lens, the considerable magnitude of the accommodation, the preferential development of the rod system, the high coefficient of morphological summation of the neuronal elements of the retina, etc. (F. V. Andreev, 1986; G. L. Kooyman and H. T. Andersen, 1969; S. Wilson, 1970; J. Lythgoe and H. Dartnall, 1970; G. Jamieson and H. Fisher, 1970. 1971. 1972; A. Nagy and K. Ronald, 1972). In addition, the pinnipeds possess a very high visual acuity (R. J. Schusterman et al., 1965; S. H. Feinstein and C. E. Rice, 1966; R. J. Schusterman and R. F. Balliet, 1970, 1971; R. J. Schusterman, 1972). Steller's sea lion, the Californian sea lion and the common seal distinguished objects, under water, with angular dimensions of 5–9°. On the other hand, blind animals in a normal state of nutrition are encountered under natural conditions, for example - of the Southern elephant seal (J. H. Sorensen, 1950). Up until the present time it is still not clear as to which sensory organs an animal with a damaged visual analyzer utilizes for orienting itself properly in the natural environment and for hunting successfully. One of the suggestions is the occurrence of echolocation in pinnipeds.

Generation of sounds by pinnipeds. Like the cetaceans, pinnipeds are capable of producing two different sound signals simultaneously, which presupposes the presence of two independent sound sources (K. S. Norris, 1969). The vocal cords of pinnipeds, located in the larynx, are well developed (G. Kelemen, 1963; S. Odend'hal, 1966). Cutting them in the Californian sea lion deprived it of the possibility of producing sounds (B. Eiseman et al., 1965). The participation of the larynx in sound production was also corroborated in later studies (R. J. Schusterman, 1967). The use of a triangulation technique made it possible to demonstrate the participation of the anterior part of the larynx in the production of the barking sounds, and of the posterior section of the pharynx in the production of the clicks (T. C. Poulter, 1965). In this study the Californian sea lion was also utilized as the experimental animal. Later a hypothetical model was proposed for the functioning of the dorsomedial pouch of the larynx in the production of the clicks (S. Odend'hal, 1966). This model obtained some corroboration in that the click frequency of the sea lion increased by approximately an octave after the animal breathed a mixture of 80% helium and 20% oxygen (R. W. Brauer et al., 1966).

Perception of sounds by pinnipeds. Studies on the anatomical structure of the ear of pinnipeds have shown that the changes, in comparison with the structural plan of the auditory apparatus of terrestrial mammals, are expressed to a lesser degree than in the cetaceans (B. Møhl, 1964; C. A. Repenning, 1972). One such difference is that the auditory ossicles are markedly separated from the cranium by the enlargement of the foramen lacerum and the f. petrooccipitalis. This indicates that osseous permeability of sounds plays a smaller role in the reception of the sound signals by pinnipeds, than is the case in terrestrial animals. The absence of acoustic isolation adaptations of the cetacean type and the developed capability of pinnipeds for localizing the source of a sound indicate that evidently not all of the adaptations, which allow determination of the direction of sound under water, have been described. There are two hypotheses regarding this question. The first proposes an adaptation of the middle ear, consisting of an increase in the rigidity of the conducting apparatus, which increases the sensitivity to the intensity of the sound (B. Møhl, 1964). The second speaks of adaptations at the level of the hearing centers to small differences in time of the arrival of the signal to the right and left ears (R. L. Gentry, 1967).

A study of the structure and function of the external acoustic meatus in the eared seals and the true seals (N. V. Lipatov, 1985 a, b) has made it possible to arrive at the following interesting conclusions: 1) the air remaining in the external auditory meatus of the true seals when the animals submerge in water is one of the links in the sound conducting channel; 2) in the true seals the hearing thresholds under water, at least in the range of the optimal sensitivity, are determined by the tympanal conduction rather than by the osseous conduction; 3) the capacity for closing the external auditory pore and preserving the air in the external auditory meatus when submerged in water is an adaptation which arises in the process of evolution with the transition of the animals to an aquatic way of life; 4) the fur covering of the eared seals, as a result of the air layer remaining in it

(E. V. Romanenko and E. V. Sokolov, 1986), comprises a considerable obstacle to sound waves with frequencies higher than 1 kHz; 5) sound in the eared seals is perceived by the concha auriculae, rather than by the auditory meatus, as in the true seals, which indicates that the tubular conchae auriculae are also an adaptation to the aquatic way of life. Some of these propositions have been confirmed experimentally on man (N. V. Lipatov, 1985 v).

A study of the perception of sound signals by the Caspian seal in air and under water has made it possible to assume, firstly, the direct passage of sound from the anterior direction through the tissues of the head to the proximal portion of the external auditory meatus, in accordance with the theory (N. V. Lipatov and G. N. Solntseva, 1974; N. V. Lipatov, 1985 a, b, v), and, secondly, an indirect passage of the acoustic signal (A. G. Kupin, 1986). In this case, in the opinion of the author, the acoustic signal passes along the following path: through the skin of the body, the tissue of the body and neck to the proximal section of the external auditory meatus, and to the inner ear. In this case there was noted a weakening of the signal, by a factor of 1.5–2, as compared with the direct passage. The presence of a similar indirect pathway of sound conduction through the tissue of the neck, a sound-conducting band of tissue, has also been proposed by other authors (E. A. Perry and D. Renouf, 1988; B. Møhl, as cited by D. Renouf, 1989). In their opinion, such a structure allows a seal that is on the surface to perceive not only air-borne but also underwater sounds, which markedly improves the localizability of the sound.

Pinnipeds possess well developed underwater hearing in a wide range of frequencies. Thus, the harp seal has an elevated sensitivity to acoustic signals in the frequency range of 2–22.9 kHz (J. M. Terhune and K. Ronald, 1972). In the ringed seal one finds approximately the same sensitivity (± 7 dB) to frequencies of 1–45 kHz (J. M. Terhune and K. Ronald, 1975) with an upper limit of perceived frequency at 60 kHz (J. M. Terhune and K. Ronald, 1976). The common seal well perceives sounds with frequencies of 1–32 kHz, with an upper limit of perception at 55 kHz (B. Møhl, 1967, 1968). The upper limit of perception of sound signals in the Californian sea lion falls on a frequency of 34 kHz (R. J. Schusterman and P. W. Moore, 1978). This animal also well differentiates the intensity of sound (about 3 dB at a frequency of 16 kHz) (P. W. Moore and R. J. Schusterman, 1978). Under the water the Northern fur seal most clearly perceives sounds that have a frequency of 2–32 kHz, while above 36 kHz the threshold of sensitivity increases markedly (R. J. Schusterman and P. W. Moore, 1978). The maximal sensitivity of hearing in this species falls in the frequency range of 12–16 kHz (G. L. Zaslavskii and V. A. Novikov, 1978).

In air an increased sensitivity to acoustic signals in the Californian sea lion occurred in the frequency region of 2–16 kHz, in the Northern fur seal — from 2 to 20 kHz (R. J. Schusterman and P. W. Moore, 1980), in the common seal — from 2 to 16 kHz (B. Møhl, 1968) and in the Caspian seal — from 8 to 12 kHz (A. G. Kupin, 1986).

Furthermore, pinnipeds possess a highly developed capacity for determining the direction of acoustic signals under water. This was shown for the common seal (B. Møhl, 1968) (the resolution comprised 2° when the frequency of the signal was 2 kHz). Later studies, carried out with this same species, corroborated the data obtained (9 ± 4° at a signal frequency of 3-4 kHz) (J. M. Terhune, 1974). The Californian sea lion also well determined the direction of acoustic signals under water; the resolution comprised 15° with a signal frequency of 3.5 kHz (R. L. Gentry, 1967) and 9° at a frequency of 1 kHz (P. W. Moore, 1975 P. W. Moore and W. W. Au, 1975).

Thus, the hearing of pinnipeds is highly adapted to the conditions of the aquatic medium and, on the whole, the pinnipeds possess the necessary physiological prerequisites for making use of acoustic signals for purposes of orientation and echolocation.

At the present time the functions of the acoustic activity in air of the polygamous species of pinnipeds have been elucidated to a considerable degree. A considerable number of studies have been devoted to the role of sound signals in the territorial, reproductive and play behaviour of these animals, although not all species have been studied to an equal degree. Apparently, acoustic signalization in air is one of the principal mechanisms for the establishment and maintenance of the structure within the population.

The duration of the most typical sounds, resembling a short howl, barking, coughing and tussive sounds, varies from 0.02 to 3 s, and in this case the short signals of 0.02–0.6 s are usually produced in series (3–16 signals). The major part of the energy of the signals of the mature males of most species falls in the frequency range of 0.1–0.5 kHz. The sound signals of the females and young animals are of a higher frequency. The maximal frequency of the airborne acoustic signals of pinnipeds is 4–7 kHz.

Less light has been shed on the role of the sound signals produced in air among the true seals.

The question of the functional significance of the sounds produced by pinnipeds underwater should also not be considered as having been definitively decided. Early evidence on the use of acoustic signals for purposes of echolocation (W. E. Evans and R. M. Haugen, 1963; T. C. Poulter, 1963, 1966, 1969; H. N. Schaver and T. C. Poulter, 1967; T. C. Poulter and R. A. Jennings, 1969; T. C. Poulter and D. C. Del Carlo, 1973; D. Renouf and M. B. Davis, 1982) has been called into question (R. J. Schusterman, 1968, 1981; D. Wartzok et al., 1984). Control studies have not corroborated the use by seals of the principle of active echolocation for purposes of orientation (R. J. Schusterman, 1967; B. L. Scronce and S. N. Ridgway, 1980), although one must take into consideration that under conditions of captivity many species of pinnipeds and cetaceans may considerably change the character of their acoustic activity.

From an examination of the way of life of some seals it is possible to select the pinniped species that are of greatest interest with regard to further experiments on echolocation. Thus, studies on the Weddell seal indicate that these animals are often encountered in cracks in ice fields, at a distance of several tens of kilometers from the open parts of the sea (A. G. Tomilin, 1965; C. Ray and D. O. Lavalee, 1964; C. Ray, 1970). It is difficult to explain these cases by the ability of the seals to move over the ice. The speed of such movement in most seals may be as much as 5–10 km/h. Such a speed, however, is possible only over short sections of the path. Furthermore, the animals would have to overcome tens of kilometers amidst accumulations of ice, under conditions in which their usual methods of orientation would be greatly hampered.

On the other hand, the seals could reach such cracks by moving under the ice, in spite of the tremendous thickness of the latter (up to 200–300 m). The depth to which Weddell's seals were able to dive was established by means of a special manometer. This depth was found to be 300–400 m (DeVries and Wohlschlag, 1964; G. L. Kooyman, 1965). However, over the average time of a dive (10.5 min) the seals are able to swim only about 2.2 km (J. L. Littlepage, 1963). Thus, in order to successfully overcome a distance of 30–50 km, the seals must make use of intervening cracks. In order to find these under the thick layer of ice under conditions of darkness, it is necessary to have a developed system of echolocation (A. G. Tomilin, 1965). The study of the repertoire of the underwater sounds of this animal indicates a possible use of some of them for purposes of echolocation (C. Ray, 1965; J. Thomas and V. Kuechle, 1982).

No less promising in this regard also is the spotted seal, as well as subspecies of the common seal, some populations of which feed and orient themselves in very turbid water.

In the opinion of A. G. Tomilin (1965) the use of the principle of active echolocation would be of vital importance also to the Arctic seals (ringed seal, bearded seal), which have to move under the ice and find the breathing holes, and also catch their prey under the conditions of the prolonged polar night.

Vocalizations in the animals often tend to be associated with a certain degree of excitation, that is higher at a given moment of physiological activity (E. Duffy, 1957; R. J. Andrew, 1962, 1964). It has been proposed that the underwater clicks emitted by the California sea lion may be associated both with the overall state of stimulation as well as with a manifestation of an "orientation reaction" (R. J. Schusterman, 1966) and, as a consequence of this, they may occur functionally as a part of the communication system (R. J.. Schusterman et al., 1966). Studies on the effect of different stimuli on the underwater acoustic activity (the experiments were carried out under conditions of captivity) have shown that the underwater clicks and other underwater sounds of the sea lion are indeed associated with social and seeking behaviour (R. J. Schusterman et al., 1966, 1967). Furthermore, the barking sounds were specifically associated with the aggressive and hierarchical behaviour of the sea lion, and they played a large role in the acquisition and maintenance of a territorial area in the holding tank (R. J. Schusterman and R. G. Dawson, 1968; R. J. Schusterman and R. F. Balliet, 1969). It was established that sounds of this type produced by the largest male restricted the movements and vocalizations of the other smaller males and apparently, on the whole, they diminish the probability of physical encounters between the animals (R. J. Schusterman and R. F. Balliet, 1969).

Also associated with the state of excitation and aggression are some sounds produced by the Weddell seal. A. A. Lindsay (1937), who observed and recorded the vocalizations of these animals in air and under water, noted that the seal produced long trills of pulsed signals when it was agitated. When the recorded sounds were played back in a holding tank to other animals of this species, they answered the threatening trills with similar series of pulsed signals (W. A. Watkins and W. E. Schevill, 1968). The duration of the answering trills was approximately equal to the duration of the trills that were played back in the holding tank.

Since many seals and sea lions become more vocal under water in the reproductive season (W. E. Schevill et al., 1966; J. Stirling, 1973; W. A. Watkins and W. E. Schevill, 1979), it is probable that the underwater sounds of pinnipeds are utilized for purposes of reproductive behaviour.

Underwater acoustic signals are also used for maintaining contact between mother and young during the period of feeding (E. Perry and D. Renouf, 1988). The young of the common seal produced a calling cry which could be heard above water and which induced an appropriate reaction in the female (W. E. Evans, 1967). After the young animals changed over to independent feeding (at an age of 4–6 weeks) they ceased producing such signals.

Thus, much like the acoustics in air, the underwater acoustical signalization of the pinnipeds plays an important role in their social organization and, very probably, it fulfills the same functions as does the signalization in the air medium.

The most widely distributed sounds that the pinnipeds produce under water are the pulsed signals (single, double and series). The duration of the individual pulses ranges from 0.005 to 1.5 s, with a frequency ranging from 0.1–16 kHz. Individual components can be traced up to 30 kHz, but there have been hardly any studies by means of sound-recording and sound-analyzing apparatus that has a wide frequency range. The major part of the energy falls in the frequency band up to 2 kHz. The repetition rate of pulses in a series differs (20–140 pulses per second), as a consequence of which are created different auditory forms, from a roar to a growl.

More rarely encountered are compound signals which are composed of pulsed and frequency modulated structures (trill, complex trill, various cries) with similar frequency and temporal characteristics.

On the basis of a survey of the available information on the acoustical activity of pinnipeds, it may be noted that almost all of the species of seals and sea lions, which have been studied with regard to their ability to produce underwater acoustic signals, produce similar sounds also in the air medium (Californian sea lion, Steller's sea lion, common seal, grey seal, Weddell's seal, etc.). Further studies will help to establish whether or not the reverse is true, although, taking into account by and large the high level of adaptation of pinnipeds to the aquatic medium, it may be assumed that all of the pinniped species are capable of generating functional underwater sounds and the problem lies only in the inadequacy of our knowledge. Thus it is known that the highly polygamous Northern elephant seal and Northern fur seal are able to produce underwater acoustic signals, although there is a lack of any detailed information about these signals (T. C. Poulter, 1963).

The overwhelming majority of sounds produced by pinnipeds, both in air as also in the water medium, are pulsed signals. It is interesting to note that the underwater signals as a whole are of a higher frequency (the major part of the energy falls on frequencies of up to 2 kHz, maximal frequency up to 16 kHz and in some individual cases up to 30 kHz) than the airborne signals (correspondingly 0.5 kHz and 4–7 kHz). Also at a higher frequency is the reception of the sounds under water (region of increased sensitivity on average 1–35 kHz), as compared with air (1–16 kHz). This is undoubtedly associated with the overall high level of adaptation of the pinnipeds to the water medium.

In conclusion it may be stated that, in spite of the fairly large number of studies on the underwater acoustics of pinnipeds, the repertoire and acoustical activity of the majority of species remain little studied, and our notions on the adaptive value of the signals are in many ways unclear. Promising and important directions of further studies are: a) comprehensive ethological and acoustical studies on different species of seals in their natural habitat; b) the study of their echolocation capability and communication in oceanarium conditions; c) the creation of standardized catalogues of the signal repertoires of different species by scientists from different countries.

Chapter 2. Characteristics of the behaviour and underwater sound signalization of the spotted seal (*Phoca largha* Pallas, 1811)

1. Underwater acoustic activity of the spotted seal.

In their initial stage our studies of the spotted seal, from two remote points of the distribution range, mainly concerned the characteristics of the underwater acoustical activity during the searching and hunting behaviour of the seals. The studies were carried out during the summer and autumn period, which is a period of intensive feeding of this species on the spawning runs of salmon (July–October, 1980–1983). At the same time we have noted some characteristics of the distribution of the spotted seal. On Kamchatka the region of observations included the estuarine areas of the Ozernaya, Opala and Bol'shaya rivers, and the coastal area of the sea between the estuaries of these rivers, while in the Amur liman the observation region includes a portion of the littoral area of the Amur liman in the vicinity of the Ozerpakh settlement.

A. Kamchatka spotted seal.

a. Seasonal and diurnal dynamics of distribution

As the study of the distribution of the spotted seal in the region of the Ozernaya and Opala rivers has shown, there exists a definite seasonal dynamic pattern in the distribution of the seals in the marine coastal area (V. M. Bel'kovich and M. N. Shchekotov, 1989). Thus, in July 1982 most of the animals (about 400 individuals – Ozernaya river; about 2 thousand individuals – Opala river) were concentrated in the estuaries, disposed in a dense group at a distance of up to 300 m out to sea. The closely positioned animals in such accumulations (distance between individual animals – 5–10 m) formed a distinctive "live net" barring the entry into the river. Furthermore, in the Opala river a large number of animals (100–200 individuals) were noted during the high tide in the river itself, up to 2 km from the mouth. Regular inspections of the coastal area of the sea on both sides of the estuaries of the rivers (up to 20 km) showed that at this time only a few individual animals were encountered there. It is very probable that such a distribution of the spotted seal is associated with the small numbers of fish (start of the sockeye salmon run) and a behavioural adaptation to this of the seals, since in the dense groups of animals more favourable conditions are created for catching the fish.

In August-September the distribution of the spotted seal changes in the coastal zone. The seals are distributed almost evenly in the area in front of the estuary up to 600–700 m from the shore. The distance between the individual animals also increases (15–50 m). Furthermore, a considerable number of animals (150–200 individuals in total) are encountered in the sea along the coast at distances of up to 15–20 km from the mouth of the river. For their hunting, the animals made use of local features of the topography of the shore line. Near the pebble spits, which protruded 30–50 m out to sea, there were constantly present groups of seals of 5–12 individuals, and in some cases of up to 50 individuals. Thus, with the increase in the availability of the food objects towards the end of the summer - beginning of the autumn, the distribution of the spotted seal in the coastal area becomes more even.

The daily dynamics of the displacements of the spotted seal in the "river-sea" system are found to be greatly affected by the tidal phenomena, because of the differing intensity of the salmon run at high tide and low tide. The salmon (chum, coho) ascend up the river en masse only during the rising tide. During the ebb tide the absence of the fish run led to the situation that most of the seals that were located in the sea "rested", in a location where they were not disturbed by the flow of the river (Figure 3). The characteristic state in this case was the "rest-sleep", in which the animal stretched out its neck, raising the tip of its snout, and closed its eyes. According to the observations in the estuary of the Opala river, the duration of such "sleep" varied depending on external factors: ebb tide (calm) - 122.1 ± 12.26 s, ebb tide (cutter, helicopter) - 12.2 ± 3.22 s, beginning of rising tide (movement of animals to the estuary) - 19.5 ± 4.49 s, rising tide (calm) - 36.0 ± 5.94 s. After each period of "rest sleep" the seal looked around, usually for 3–10 s, and then "fell asleep" once more.

The spotted seal may also rest ("sleep"?), while located "like a log" right at the surface of the water (on its back, on its belly, on its side) without moving.

3–4 hours prior to the rising tide (and up to the beginning of the entry of the fish into the river) a mass-scale and unhurried movement of the animals was observed from the resting place to the mouth of the river, with periods of short rest. "Sleep" during the rest was repeated 5–12 times, lasting for 5–20 s; in the intervals between the "sleep" the seal looked around for 5–25 s; Thus, the total rest time comprised 1-2 min, after which the seal once again moved towards the mouth of the river, in some cases along the surface of the water.

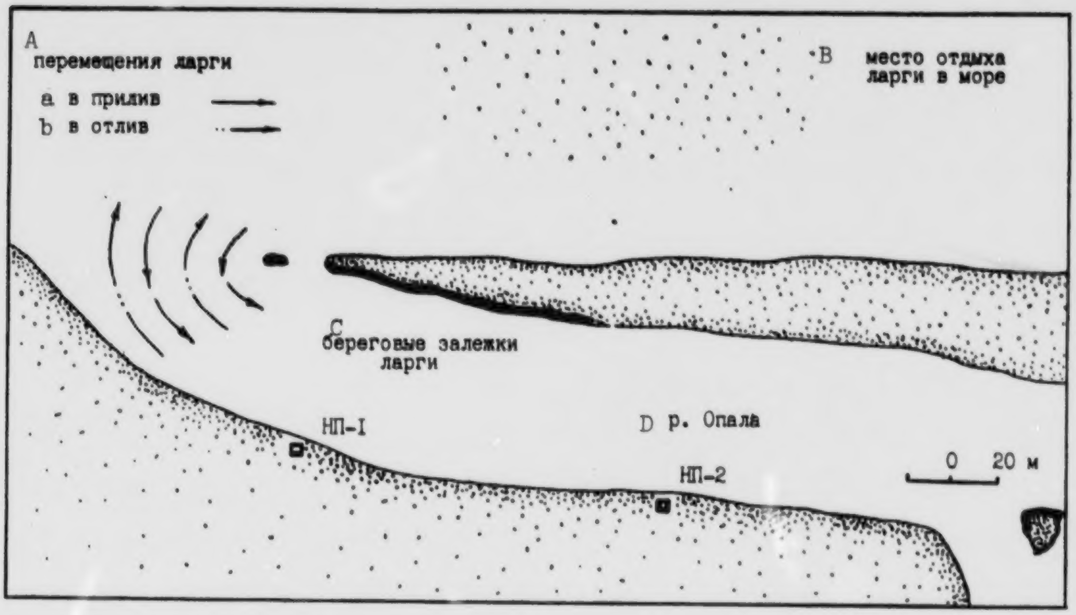


Рис.3.Схема района наблюдений (р. Опала, сентябрь 1982 г.)

Figure 3. Schematic map of region of observations (Opala river, September 1982)

A - movements of spotted seal
  a - during rising tide, b - during ebb tide
B - resting location of spotted seal in the sea
C - on shore hauling-out sites of spotted seal
D - Opala river
НП-1, НП-2 - NP-1 and NP-2 - Observation posts 1 and 2

During the rising tide the animals actively moved upstream, against the flow of the river, sometimes in the process swimming on the surface of the water. The hunting activity was especially great in the shallows of the river near the shore and was observed for up to 600–800 m from the mouth of the river. During the ebb tide the markedly strengthened flow of the river "drove out" the seals from the river into the sea. As a rule during the low tide also the spotted seals may form on-shore rookeries in the mouths of the rivers (V. N. Burkanov, 1982). In the region of the Opala river an on-shore rookery of the spotted seal was formed on a sand spit (Figure 3), predominantly during the night time. On it there were usually located 300–500 individuals of various ages, and in some cases up to 2 thousand. The animals were disposed at a high density, with the distance between them being no more than 40–50 cm. Sometimes the rookery persisted also during the day, though the number of animals on it was considerably diminished (by 50–70%). The seals rested for most of the time. The adult individuals manifested aggressive behaviour mainly when animals attempted to settle themselves more comfortably and when new animals came out onto the shore. The animals made abrupt lunges with their head, barely opening their mouths, and threatening movements with one of their fore flippers, and they also emitted acoustic signals of varying duration, resembling howling. On the whole, however, the social interactions on the hauling-out grounds were expressed only to a slight degree; there are practically no stable relationships between the individuals. As has been shown by special studies on the hauling-out grounds of the common seal, which is closely related to the spotted seal, the most stable social interrelationships are observed only in the "mother-young" pairs (J. Goodsell, 1987).

The "sleep" state during resting was expressed by a limpness and immobility of the animal, during which condition its eyes were closed. When the numbers of spotted seals comprised 100–200 individuals the duration of the "sleep" was 2–35 s, averaging 7.5 ± 2.50 s, after which the seal looked around for 3–15 s, with an average of 3.9 ± 1.54 s, and then again "fell asleep". With small numbers of animals on the hauling-out grounds the sleep time did not exceed 2–5 s, while the looking-around time increased considerably, to 10–35 s, with an average of 17.2 ± 2.78 s. An increase in the rest and sleep time in large groupings of the common seal , as compared with small groups, has also been noted by Canadian investigators (M. Krieber and C. Barrette, 1984).

At a distance of 1.2 km upstream along the course of the Opala river a "juvenile" rookery of 70–80 young animals was located on an island (Figure 3). Their play behaviour was accompanied by sound signals, resembling those of the adult animals, and it included rushes, lunges and chases. Their "sleep" lasted for no more than 2–10 s and. in general, these animals behaved in a more watchful fashion on their hauling-out grounds than the adult seals.

b. Sound signals

A spectral-temporal and auditory analysis of more than 16 thousand signals of the Kamchatka spotted seal allowed us to distinguish and describe nine principal classes of sound signals (Table 1).

Table 1

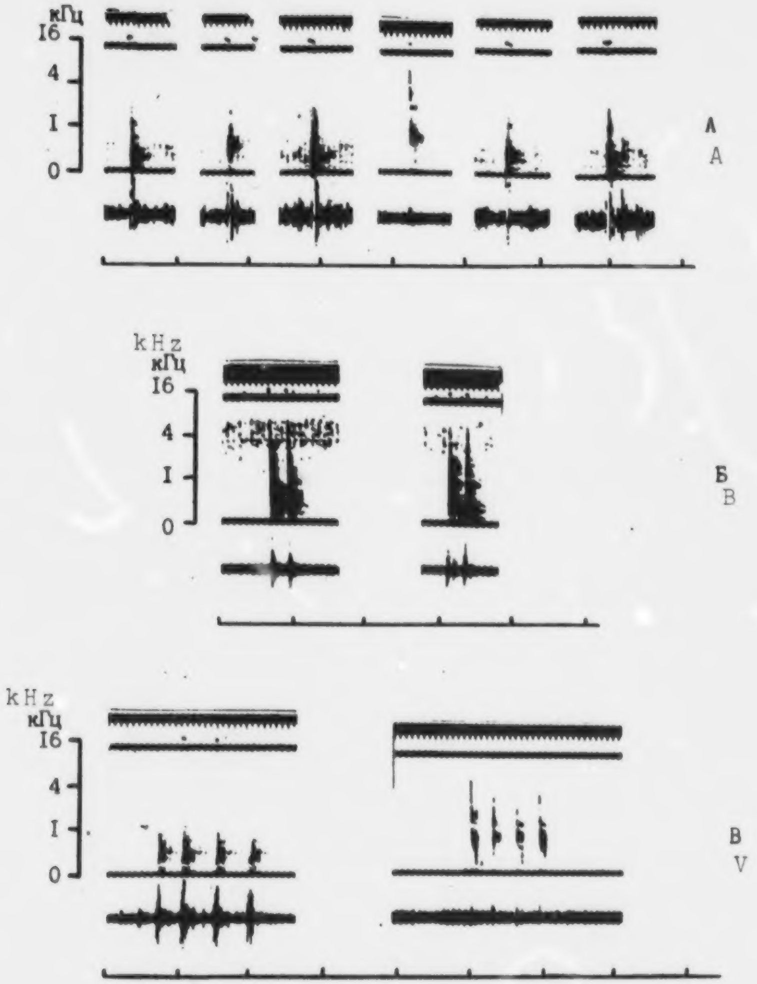
Principal classes of acoustic signals of the Kamchatka spotted seal (July–September 1981 and 1982)

Name of class	Number of signals	% of total number of signals	Number of signals spectrally analyzed
1. "Single pulsed signal"	5108	30.8	82
2. "Double pulsed signal"	3617	21.8	88
3. "Short series of pulses"	1699	10.3	36
4. "Long series of pulses"	3191	19.2	37
5. "Champing"	601	3.6	18
6. "Ua", "Uo"	1430	8.6	42
7. "Squeak"	519	3.2	13
8. "U", "Uk"	320	1.9	13
9. Other	99	0.6	6
Total	16584	100	335

Some frequency-temporal characteristics of the principal classes of signals of the Kamchatka spotted seal are presented below.

1. "Single pulsed signal". Duration of pulses varies from 0.005 to 0.06 s. Dominant frequency of most signals — 0.2–1.6 kHz. Frequency range of pulses 0.2–8.0 kHz, in some signals — 0.2–16 kHz (Figure 4A).

2. "Double pulsed signal". Total duration of signal 0.03–0.09 s. The duration of individual pulses ranges from 0.005 to 0.03 s. Interval between pulses is 0.005–0.05 s. Dominant frequency of signals 0.2–1.2 kHz. Frequency range 0.2–8.0 kHz, in some signals — 0.2–16 kHz (Figure 4B).



Время: I деление - 0,2 с
Time: 1 division - 0.2 s

Рис.4.Звуковые сигналы ларги основных классов; А - № I;
Б - № 2; В - № 3.

Figure 4. Principal classes of sound signals of the spotted seal:
A - No. 1; B - No. 2; V - No. 3.

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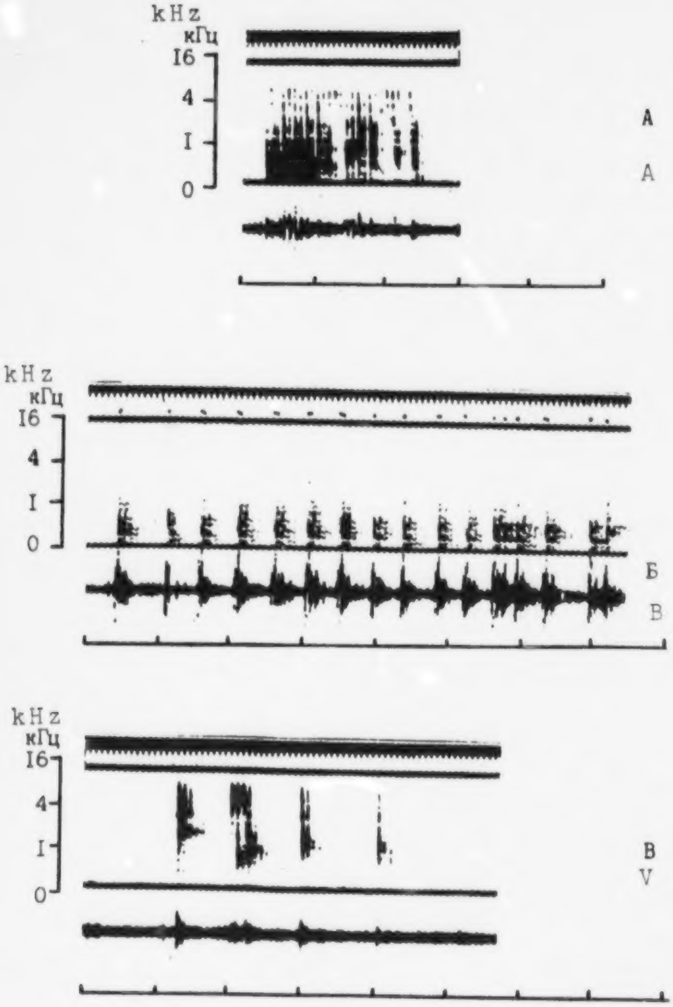
3. "Short series of pulses". Series of pulses (3–6) with a duration of 0.08–0.62 s and a repetition rate of 8–38 pulses per second. The duration of the individual pulses is 0.005–0.04 s, while that of the interval between pulses is 0.01–0.08 s. Dominant frequency in frequency band 0.2–1.2 kHz. Frequency range — 0.2–7.0 kHz, of some series — 0.2–15.0 kHz (Figure 4V).

4. "Long series of pulses". Numerous (7–27), prolonged up to 1.5 s, series of pulses with a repetition rate of 12–67 pulses per second. Duration of individual pulses — 0.005–0.06 s, of interval between pulses — 0.005–0.08 s. Dominant frequency of majority of impulses — 0.2–0.6 kHz. Frequency range — 0.2–5.0 kHz. The series may be made up both of pulses that are approximately uniform in their frequency-temporal characteristics, with almost equal intervals between the pulses, as well as of heterogeneous pulses with varying intervals between the pulses (Figure 5A).

5. "Champing". Series of single or double pulses (2–8), with a duration of 0.22–1.10 s, with a repetition rate of the single or double pulses of 4 to 12 pulses per second. Duration of individual pulses — 0.005–0.04 s, duration of interval between them — 0.04–0.14 s. Dominant frequency of pulses in the following frequency intervals: 0.2–0.4 kHz (17% of total number of pulses); 0.4–1.0 kHz (52.1%); 0.8–1.6 kHz (22.4%); 1.5–2.2 kHz (8.5%). In the elements of the series made up of two pulses the first pulse has the major part of its energy in the 0.2–0.7 kHz band. In the second pulse the region of the major part of the energy may be displaced into the wider range of 0.4–2.2 kHz. The maximal value of the dominant frequency in the series displays no evident pattern, in pulses with any ordinal number. The regions with the major part of the energy in neighbouring pulses differ only slightly, by 0.2–0.7 kHz, and not infrequently two or three successive pulses may have approximately the same values of the dominant frequency. Frequency range of series — 0.2–7.0 kHz, in some cases — 0.2–9.0 kHz (Figure 5B).

6. "Ua", "Uo". Signals with a duration of 0.04–0.12 s, composed of 2–7 closely following pulses, which sometimes merge together. Interval between pulses — 0.005–0.025 s. The pulses may be combined into two groups, with an interval between groups of 0.005–0.03 s. Duration of individual impulses — 0.01–0.03 s. The region of the dominant frequency in the second half of the signal is of a higher frequency, by 0.2–0.6 kHz, than in the first half. From this arises the effect of the auditory perception of the two sounds "u-a". In the first part of the signals the dominant frequency occurs in the following frequency intervals: 0.2–0.4 kHz (23.3% of the total number of signals) and 0.3–0.8 kHz



Время: I деление - 0,2 с

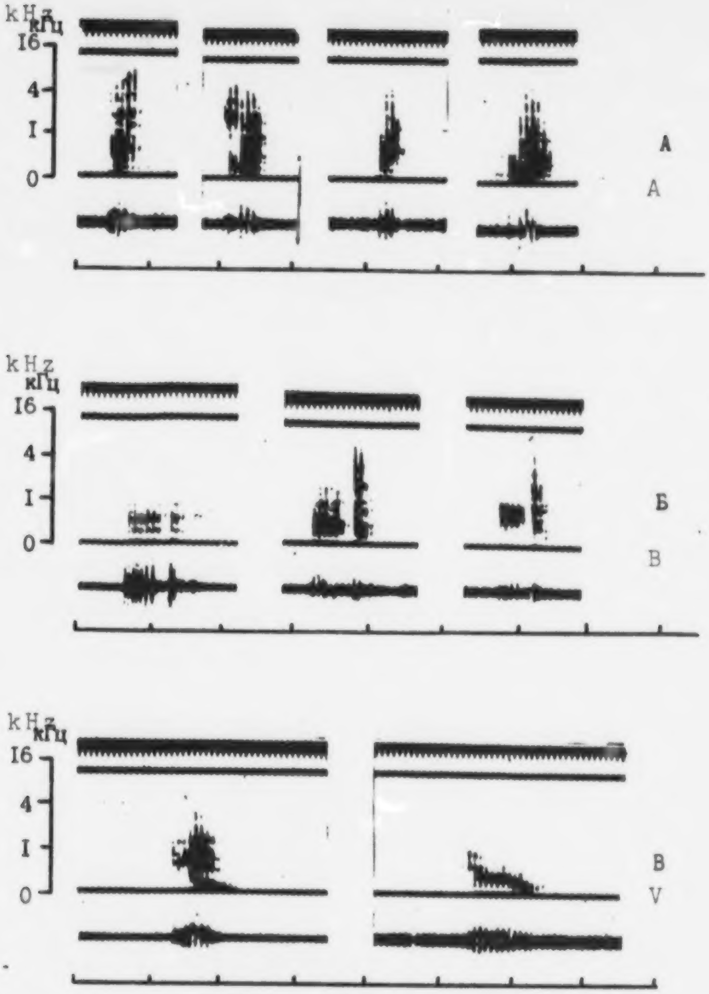
Time: 1 division - 0.2 s

Рис.5.Звуковые сигналы ларги основных классов:А,Б - № 4; В - № 5.

Figure 5. Principal classes of sound signals of the spotted seal: A, B — No. 4; V — No. 5.

(76.7%); in the second part — in the following: 0.4–0.8 kHz (60.9%); 0.8–1.0 (32.6%); 1.1–2.2 (6.5%). The frequency range of the signals is 0.2–5.0 kHz, in some cases — 0.2–16.0 kHz (Figure 6A).

7. "Squeak". Short series (0.11–0.17 s), composed of 5–7 pulses, with a duration of 0.005–0.01 s (repetition frequency of 56–100 pulses per second), with a following,



Время: I деление - 0,2 с

Time: 1 division - 0.2 s

Рис.6.Звуковые сигналы ларги основных классов: А - № 6; Б - № 7; В - № 8.

Figure 6. Principal classes of sound signals of the spotted seal: A - No. 6; B - No. 7; V - No. 8.

after an interval of 0.01–0.065 s, more powerful concluding pulse, with a duration of 0.01–0.03 s. The major part of the energy of the pulses in the first part of the signal is concentrated in the frequency intervals of 0.3–0.6 kHz and 0.5–1.2 kHz, while that of the concluding pulse — 0.3–1.0 kHz and 0.5–1.6 kHz. Frequency range of signals — 0.2–5.0 kHz, in several cases — 0.2–8.0 kHz (Figure 6B).

8. "U", "Uk". For the most part single, rarely double with an interval of 0.01 s, signals with a duration of 0.035–0.2 s, made up of two and more merging pulses. The duration of the individual pulses is 0.02–0.07 s. The regions of the dominant frequencies of the signals are 0.2–0.4 kHz, 0.4–0.6 kHz and 0.4–1.0 kHz. In the second part of the signals may be found a decrease of the dominant frequency to 0.1–0.3 kHz. The frequency range of the signals is 0.2–4.0 kHz, in some cases — 0.2–5.0 kHz (Figure 6V).

9. Other signals. Signals of the "howl" class comprise long (0.42–3 s) series of pulses, which are repeated at a rate of 80–150 pulses per second. The major part of the energy is in the 0.2–0.6 kHz and 0.9–1.4 kHz frequency band. The maximal frequency of the signals is 2 -3 hHz. These signals are apparently emitted in air and they penetrate into the aquatic medium through the body of the half-submerged animal. Another rare signal is the "bleating". The duration of the analyzed signal comprised 0.63 s. The signal comprises a series, made up of seven pulsed bursts, with a duration of 0.03–0.07 s, and with 2–7 merged pulses in each. The major part of the energy is concentrated in the frequency intervals of 0.2–0.3 kHz, 0.4–0.5 kHz and 0.7–1.3 kHz.

c. Situational changes in the acoustic activity

Below are presented short descriptions of some situations in which recordings of the signals were made and the characteristics of the underwater acoustic activity of the Kamchatka spotted seal in different sections of the habitat:

Situation I , Ozernaya river (1981 -1982). This situation may be characterized as a searching and hunting activity of 2–3 seals in a small sector of water, of approximately 600 sq. m in area (Figure 7). No combined actions of the animals were observed in this case. The eating of the fish occurred on the surface of the water. The seals were noted on this sector of water only during the rising tide. The recording was carried out from a pier on the shore.

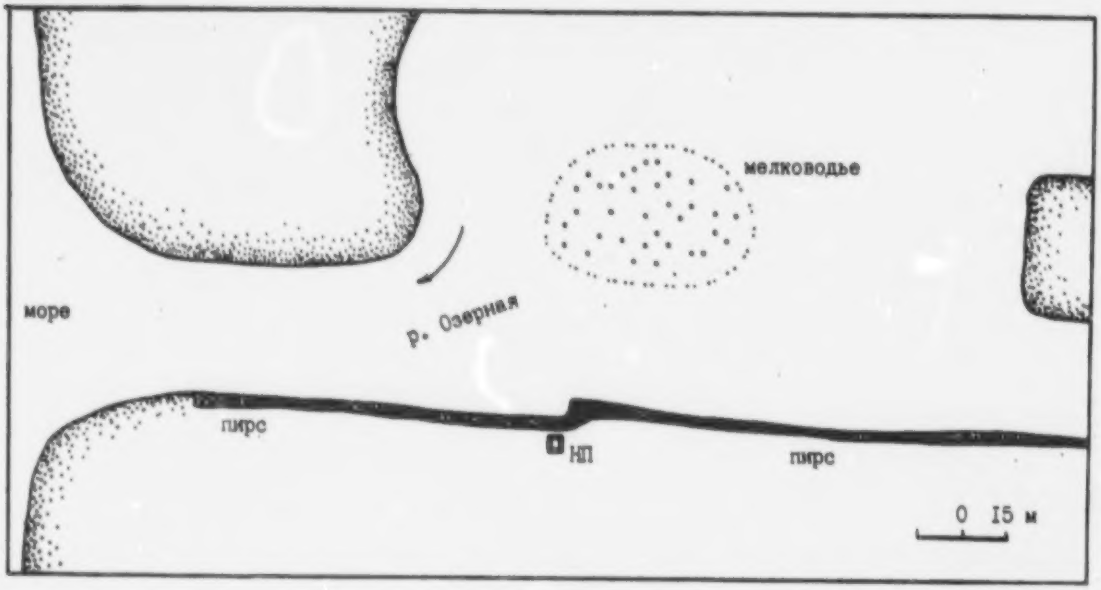


Рис.7.Схема района наблюдений (р. Озерная, Камчатка, июль-октябрь 1982, 1986 гг.)

Figure 7. Schematic map of region of observations
(Ozernaya river, Kamchatka, July–October 1982, 1986)

море - sea
р. Озерная - Ozernaya river
мелководье - shallow water
пирс - pier
НП - NP - observation post

As was shown by direct observations on the behaviour of the spotted seal under water, with the simultaneous audio-monitoring of the sector of water (data from 1986 season, see below), as well as the data from the auditory analysis of the recordings, the signals are usually produced in the form of a sequence by 1–2 individuals, and in this case the signals in each particular sequence have approximately the same intensity. The last signal in a sequence was considered to be the signal after which over the course of 30 s (a time interval 10–20 times greater than the average interval between signals in sequences of various types) not even one signal was produced.

In the analysis of the characteristics of the acoustical signalization of the Kamchatka spotted seal in this and the following situations we paid attention to the size of the sequences (the number of signals that made up the sequence, for example, Table 2) and to how the comparative share of the principal classes of signals changes in sequences with different numbers of signals (for example, Table 3). These parameters, in our opinion, are most interesting for the following comparison of the situations.

The number of recorded sequences of acoustic signals of the Kamchatka spotted seal and the relative share of all classes of signals in sequences with different numbers of signals are presented in Table 2.

Table 2

Character of the production of acoustic signals
by the Kamchatka spotted seal in Situation I

Number of signals in sequence	Number of sequences of a given type	% of total number of sequences	Number of signals in sequences of a given type	% of total number of signals
1–4	88	61.5	157	20.8
5–10	33	23.1	234	31.0
more than 10	22	15.4	363	48.2
Total	143	100	754	100

The numbers of the principal classes of signals of the Kamchatka spotted seal in sequences with different numbers of signals and their relative share are presented in Table 3.

Situation II , Bol'shaya river (1982). Searching and hunting activity of 10–15 seals in the river, at a distance of 60–70 m from the mouth. The animals individually actively pursued the fish that were running upstream with the rising tide. The recording was done from a boat, standing at anchor.

The number of recorded sequences of acoustic signals of the Kamchatka spotted seal and the relative share of all classes of signals in sequences with different numbers of signals are presented in Table 4.

Table 3

Relative share of the acoustic signals of the Kamchatka spotted seal in sequences with different numbers of signals (Situation I, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences							
	1–4		5–10		more than 10			
	P	%	P	%	P	%	Total signals	%
1. "Single pulsed signal"	59	37.6	55	23.5	104	28.7	218	28.9
2. "Double pulsed signal"	72	45.9	141	60.3	154	42.4	367	48.7
3. "Short series of pulses"	6	3.8	7	3.0	15	4.1	28	3.7
4. "Long series of pulses"	2	1.2	9	3.9	12	3.3	23	3.1
5. "Champing"	6	3.8	8	3.4	19	5.2	33	4.4
6. "Ua", "Uo"	6	3.8	6	2.6	18	5.0	30	4.0
7. "Squeak"	4	2.6	5	2.1	17	4.7	26	3.4
8. "U", "Uk"	2	1.3	2	0.9	16	4.4	20	2.6
9. Other	0	0	1	0.4	8	2.2	9	1.2
Total	157	100	234	100	363	100	754	100

Table 4

Character of the production of acoustic signals by the Kamchatka spotted seal in Situation II

Number of signals in sequences	Number of sequences of a given type	% of total number	Number of signals in sequences of a given type	% of total number of signals
1–4	15	51.7	24	14.0
5–10	9	31.0	58	33.7
more than 10	5	17.3	90	53.3
Total	29	100	172	100

The numbers of the principal classes of signals of the Kamchatka spotted seal in sequences with different numbers of signals and their relative share are presented in Table 5.

Situation III, sector of an area in the sea (1982). Searching and hunting activity of 7-8 seals in the region of a trap net located 350–400 m from the shore. The animals held themselves in a very scattered fashion, at a distance of 100–150 m from one another. The recording was carried out from a boat, standing at anchor.

Table 5

Relative share of the acoustic signals of the Kamchatka spotted seal in sequences with different numbers of signals (Situation II, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences							
	1–4		5–10		more than 10		Total signals	%
	P	%	P	%	P	%		
1. "Single pulsed signal"	0	0	16	27.6	10	11.1	26	15.1
2. "Double pulsed signal"	22	91.6	29	50.0	62	68.9	113	65.7
3. "Short series of pulses"	0	0	3	5.2	2	2.2	5	2.9
4. "Long series of pulses"	0	0	6	10.3	8	8.9	14	8.1
5. "Champing"	0	0	0	0	2	2.2	2	1.2
6. "Ua", "Uo"	1	4.2	1	1.7	1	1.1	3	1.7
7. "Squeak"	1	4.2	2	3.5	5	5.6	8	4.7
8. "U", "Uk"	0	0	1	1.7	0	0	1	0.6
Total	24	100	58	100	90	100	172	100

The number of recorded sequences of acoustic signals of the Kamchatka spotted seal and the relative share of all classes of signals in sequences with different numbers of signals are presented in Table 6.

Table 6

Character of the production of acoustic signals by the Kamchatka spotted seal in Situation III

Number of signals in sequences	Number of sequences of a given type	% of total number of sequences	Number of signals in sequences of a given type	% of total number of signals
1–4	16	55.2	39	23.4
5–10	8	27.6	46	27.5
more than 10	5	17.2	82	49.1
Total	29	100	167	100

The numbers of the principal classes of signals of the Kamchatka spotted seal in sequences with different numbers of signals and their relative share are presented in Table 7.

Table 7

Relative share of the acoustic signals of the Kamchatka spotted seal in sequences with different numbers of signals (Situation III, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences							
	1 - 4		5 - 10		more than 10		Total	
	P	%	P	%	P	%	signals	%
1. "Single pulsed signal"	7	17.9	7	15.2	5	6.1	19	11.3
2. "Double pulsed signal"	23	59.0	29	63.0	57	69.5	109	65.3
3. "Short series of pulses"	1	2.6	1	2.2	4	4.9	6	3.6
4. "Long series of pulses"	3	7.7	4	8.7	7	8.6	14	8.4
5. "Champing"	0	0	0	0	1	1.2	1	0.6
6. "Ua", "Uo"	0	0	0	0	1	1.2	1	0.6
7. "Squeak"	3	7.7	5	10.9	7	8.5	15	9.0
8. "U", "Uk"	2	5.1	0	0	0	0	2	1.2
Total	39	100	46	100	82	100	167	100

Situation IV, Opala river (1982). Searching and hunting behaviour of 80 - 100 seals in the river, at a distance of 300 m from the mouth (Figure 3). No combined actions were observed in this case. The animals individually actively pursued the fish, moving upstream as the tide was rising. The recordings were made from the shore.

The numbers of signals recorded and their relative share are presented in Table 8.

284 signal sequences of the Kamchatka spotted seal, which did not overlap with other sequences, were selected for further analysis. The numbers of sequences of all classes of acoustical signals in sequences of differing duration and with different numbers of signals are presented in Table 9.

Table 8

Relative share of the principal classes of signals of the Kamchatka spotted seal (Situation IV)

Name of class	Number of signals	% of total number of signals
1. "Single pulsed signal"	4845	31.3
2. "Double pulsed signal"	3028	19.5
3. "Short series of pulses"	1660	10.7
4. "Long series of pulses"	3140	20.3
5. "Champing"	565	3.7
6. "Ua", "Uo"	1396	9.0
7. "Squeak"	470	3.0
8. "U", "Uk"	297	1.9
9. Others	102	0.6
Total	15491	100

Table 9

Character of the production of acoustic signals by the Kamchatka spotted seal in Situation IV

Number of signals in sequences	Number of sequences of a given type	% of total number of sequences	Number of signals in sequences of a given type	% of total number of signals
1–4	17	6.0	36	0.6
5–10	24	9.5	228	3.6
more than 10	240	84.5	6140	95.8
Total	284	100	6404	100
Duration of sequences (s)				
1–15, av. 9.3	43	15.1	193	3.0
16–30, av. 25.0	53	18.7	556	8.7
31–233, av. 81.0	188	66.2	5655	88.3
Total:	284	100	6404	100

Table 10

Relative share of the acoustic signals of the Kamchatka spotted seal in sequences with different numbers of signals (Situation IV, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences							
	1–4		5–10		more than 10		Total signals	%
	P	%	P	%	P	%		
1. "Single pulsed signal"	8	22.2	70	30.7	1669	27.2	1747	27.3
2. "Double pulsed signal"	19	52.8	75	32.9	1709	27.8	1803	28.2
3. "Short series of pulses"	0	0	15	6.6	396	6.5	411	6.4
4. "Long series of pulses"	1	2.8	40	17.5	1059	17.2	1100	17.2
5. "Champing"	0	0	2	0.9	117	2.9	179	2.8
6. "Ua", "Uo"	8	22.2	23	10.1	884	14.4	915	14.3
7. "Squeak"	0	0	2	0.9	167	2.7	169	2.6
8. "U", "Uk"	0	0	1	0.4	79	1.3	80	1.2
Total	36	100	228	100	6140	100	6404	100

Table 11

Relative share of the principal classes of signals in sequences of different duration of the Kamchatka spotted seal (Situation IV, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Duration of sequences (s)					
	1–15		16–30		31–233	
	P	%	P	%	P	%
1. "Single pulsed signal"	53	27.5	152	27.3	1542	27.3
2. "Double pulsed signal"	91	47.2	205	36.9	1507	26.6
3. "Short series of pulses"	12	6.2	31	5.6	368	6.5
4. "Long series of pulses"	24	12.4	87	15.6	989	17.5
5. "Champing"	1	0.5	10	1.8	168	3.0
6. "Ua", "Uo"	7	3.6	58	10.4	850	15.0
7. "Squeak"	5	2.6	10	1.8	154	2.7
8. "U", "Uk"	0	0	3	0.5	77	1.4
Total	193	100	556	100	5655	100

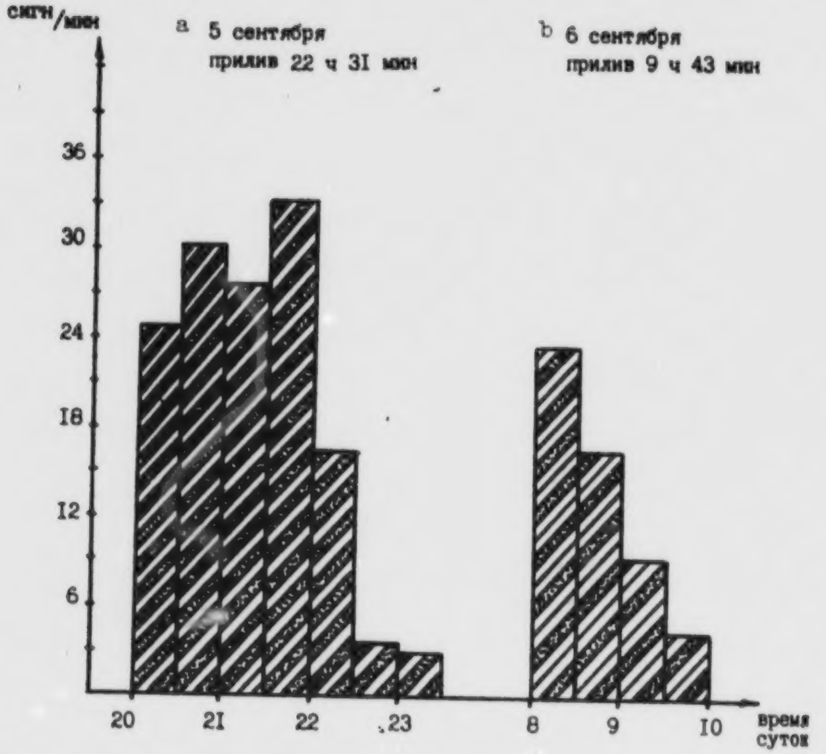


Рис.8.Динамика уровня звуковой активности камчатской ларги в прилив (р. Опала, сентябрь I982 г.)

Figure 8. Dynamics of the level of sound activity of the Kamchatka seal during the high tide (Opala river, September 1982).

ordinate - signals per minute; abscissa - time of day

a - 5 September, high tide 22 hours 31 minutes
b - 6 September, high tide 9 hours 43 minutes

The numbers of the principal classes of signals of the Kamchatka spotted seal in sequences with different numbers of signals and their relative shares are presented in Table 10.

The numbers of the principal classes of signals in sequences of different duration and their relative share are presented in Table 11.

The analysis of the dynamics of the acoustical activity in the region of the biological area of study in the Opala river indicates that a high level of the acoustical activity (21–23 signals per minute) is established 2-3 hours prior to the moment of the passage of the highest point of the rising tide, following which only 30–90 minutes later the level falls to 4-5 signals per minute (Figure 8). During the ebb tide the acoustical activity of the spotted seal practically completely ceased, in spite of the presence of the animals in the river and in the immediate vicinity of the hydrophone. The level of acoustical activity at one and the same time with regard to passage of the highest point of the rising tide was practically independent of the time of day. The analysis also did not reveal any differences in the use by the animals of the different type of signals in relation to the time of day.

Situation V , Opala river (1982). This situation was similar, on the whole, to situation IV, except that the recording was carried out from the side of a rubber dinghy as it floated downstream along the river.

The number of recorded sequences of acoustic signals of the Kamchatka spotted seal and the relative share of all classes of signals in the sequences with different numbers of are presented in Table 12.

Table 12

Character of the production of acoustic signals
by the Kamchatka spotted seal in Situation V

Number of signals in sequence	Number of sequences of a given type	% of total number of sequences	Number of signals in sequences of a given type	% of total number of signals
1–4	43	78.2	73	37.0
5–10	7	12.7	47	23.9
more than 10	5	9.1	77	39.1
Total	55	100	197	100

The numbers of the principal classes of signals of the Kamchatka spotted seal in sequences with different numbers of signals and their relative share are presented in Table 13.

Acoustic sections of the Opala river also showed the absence of sound signals during the ebb tide, in spite of the presence of a certain number of seals 30–70 m from

Table 13

Relative share of the acoustic signals of the Kamchatka spotted seal in sequences with different numbers of signals (Situation V, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences							
	1–4		5–10		more than 10		Total signals	%
	P	%	P	%	P	%		
1. "Single pulsed signal"	15	20.5	22	46.8	32	41.6	69	35.0
2. "Double pulsed signal"	51	69.9	18	38.3	32	41.6	101	51.3
3. "Short series of pulses"	4	5.5	7	14.9	6	7.8	17	8.7
4. "Long series of pulses"	0	0	0	0	2	2.6	2	1.0
5. "Champing"	0	0	0	0	0	0	0	0
6. "Ua", "Uo"	1	1.4	0	0	3	3.8	4	2.0
7. "Squeak"	0	0	0	0	2	2.6	2	1.0
8. "U", "Uk"	2	2.7	0	0	0	0	2	1.0
Total	73	100	47	100	77	100	197	100

the hydrophone. During the rising tide the acoustical activity of the spotted seal begins to be recorded only from a distance of no more than 500–600 m from the mouth of the river and is observed right up to the mouth.

Neither during the ebb tide nor during the rising tide were we able to record any underwater acoustic signals from the young of the current year. When a "juvenile" rookery (of about 75 animals) was scared off the island that was located in the river at a distance of 1.2 km from the mouth of the river, about 60 young animals were noted to be present at a distance of 10–100 m from the hydrophone (Figure 3). Nevertheless not even one signal was recorded (the recording time in this case was about 2 hours).

From the information presented above it may be noted that in aggregate in the Kamchatka spotted seal 85.7% of the total number of signals consist of signals of the No. 1, No. 2, No. 3, No. 4 and No. 5 classes (Table 1), and 52.6% of these are signals of classes No. 1 and No. 2.

Among the signals that were recorded for the Kamchatka spotted seal in Situation I the relative share of the No. 1 and No. 2 classes was greater than 70%, and the percentage of the No. 2 class signals was especially high (48.7%).

More than 80% of the total number of signals in Situation II comprise signals of classes No. 1 and No. 2, and here also the majority are signals of class No. 2 – 65.7%.

A similar pattern, with a high percentage of the No. 2 class signals (65.3%) and a small relative share of the No. 1 class signals (11.3%), is characteristic also of Situation III.

It may also be noted that in Situations I–III the Kamchatka spotted seal predominantly produces short sequences of acoustic signals (1–10 signals), the percentage of which exceeds 82–84% (Tables 2, 4 and 6), and only 15–17% is made up of sequences with more than 10 signals, although the relative share of all classes of signals emitted in the form of both the one and the other is approximately the same — 49–51%. In all of the groups of sequences (1–4 signals; 5–10 signals; more than 10 signals) the principal classes are No. 1 and No. 2, the total percentage of which comprises 83–92% in the first group. In the second and third groups of sequences the proportion of these classes is also high (71–83%), in spite of the fact that it decreases somewhat, by 5–21%, at the expense of an increase in the relative share of the other classes of signals, primarily of the signals of classes No. 5 and No. 7 (Tables 3, 5 and 7).

In the Opala river (Situation IV, Table 8) the total percentage of the signals of classes No. 1 and No. 2 comprises only 50.8%, and in this case the signals of class No. 1 make up the greater percentage (31.3%). A comparatively large share is due to the following four classes of signals: No. 3, No. 4, No. 5 and No. 6 (totaling 43.7%). A drastic change occurs in the character of the activity of the Kamchatka spotted seal in the case when the signals were recorded from a rubber dinghy which passively floated downstream along the Opala river (Situation 5). Signal classes No. 1 and No. 2 became predominant (totaling more than 86%) (Table 13).

Among the sequences of acoustic signals of the Kamchatka spotted seal in Situation IV the percentage of sequences with a duration of more than 30 s is the highest —

66.2% (Table 9); also high is the relative share of all classes of signals that were produced in the form of these kinds of sequences (88.3%). The overwhelming majority (84.5%) is made up of sequences with more than 10 signals (Table 9).

The repetition rate of all classes of signals in the sequences of acoustic signals of the Kamchatka spotted seal with a duration of 1–15 s comprises 29.3 signals per minute and decreases somewhat in sequences with a greater duration, to 26.1–23.8 signals per minute.

As we can see from Table 11, the relative share of almost all of the classes of signals in the acoustic sequences of the Kamchatka spotted seal, that are of differing duration, change insignificantly and only the share of the No. 5 and No. 6 classes of signals increases with an increase in the duration of the sequences.

B. Spotted seal of the Amur liman

a. Some characteristics of the distribution and behaviour

Situation VI , Amur liman (July–October 1980, 1983). Searching-and-hunting activity and social behaviour of 6–12 seals that were constantly present in the studied area of water. No combined actions were observed in the catching of the fish. The eating of the fish occurred on the surface. The recording of the acoustic activity was carried out from an onshore observation post. With recording from the side of a boat not one signal was noted.

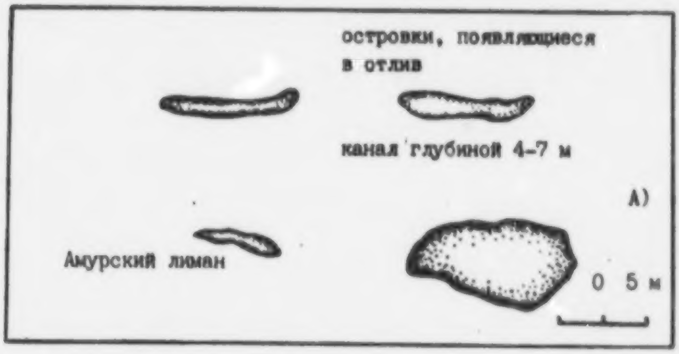
On the basis of questionnaire data, the appearance of the spotted seal in the Amur liman in the feeding locations usually occurs at the end of May, i.e. soon after the liman is freed of its ice cover. A considerable number of animals (0.5–1.5 thousand) become concentrated on the shallow-water banks, located in Schast'ya Bay and along the Sakhalinskii channel. The spotted seals also gather in the strait between Chkalova and Baidukova islands, forming large onshore rookeries (of 1–2 thousand individuals in different years), especially in the second half of the summer.

Other characteristic feeding sites for small groups (10–50 individuals) of the Amur spotted seal are shown in Figure 9. The local characteristics of the topography have a considerable effect on the movement of the fish close to the shore line (Figure 9B). Thus, the extensive bay (1) in front of the cape plays the role of a reservoir, in which linger the fish that are running close to the shore, ands after this most of these fish are forced to move along a narrow (60–70 m) channel (2) 3–5 m in depth. It is precisely in this location that favourable conditions are created for pursuing and catching fish by the seals (the large number of fish, squeezed into a comparatively narrow location, the possibility of using the shore line as a barrier for the fish, etc.).

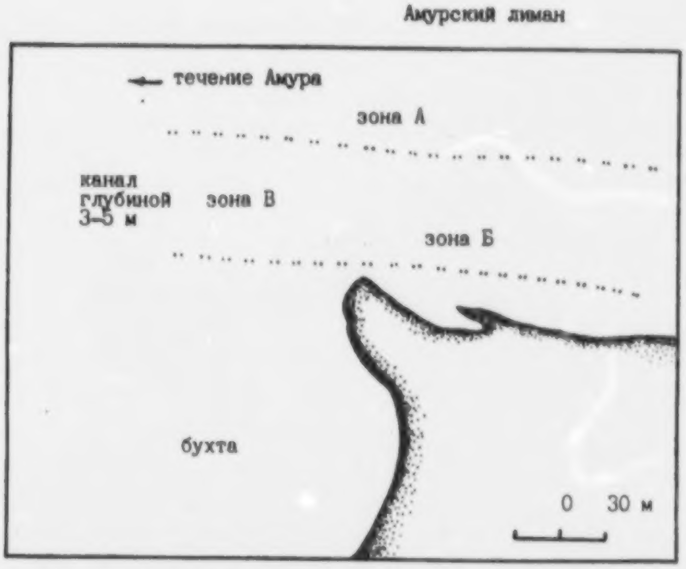
In the summer and in the autumn the distribution of the spotted seal in the liman remains practically unchanged. With the formation of the late autumn ice cover a large part of the seals depart into the Sea of Okhotsk, onto the ice edge that is advancing towards the north, and some remain to overwinter in the region of the Sakhalinskii channel.

Observations on the movements of the spotted seal in the region of the biological test area in still weather (with a calm water surface), as well as observations on an animal with a natural marker (a light-coloured patch on the head) allowed us to reveal some tactical procedures used by the animals during hunting. One may distinguish three principal stages in the searching and hunting behaviour of the seals.

The "searching" stage includes three main types of movement of the animals. The first slow movement of the seals right at the surface of the water occurs on the traverse of the cape at a distance of 60–90 m (zone A) in a direction towards the cape (Figure 9B). In this case the body of the animal is positioned at an angle to the direction of the flow of the river (with the head facing the current), which allows it to make use of the force of the river's current. If (for some reason) the animal has not started to pursue its prey, then it


островки, появляющиеся
в отлив
канал глубиной 4-7 м
А)
Амурский лиман
0 5 м

A


Амурский лиман
течение Амура
зона А
канал
глубиной
3-5 м
зона В
зона Б
бухта
0 30 м

Б

Рис. 9. Участки местообитаний амурской ларги: А) схема мелководного участка акватории вдали от берега; Б) схема участка береговой линии

Figure 9. Portions of the habitats of the Amur spotted seal: A) schematic map of shallow-water section of the area of water far from the shore; B) schematic map of section of shore line.

A островки, поябляющиеся в отлив - islands appearing at low tide.
канал глубиноя 4-7 м - channel 4-7 m in depth
Амурския лиман - Amur liman

Амурския лиман - Amur liman

B ← течение Амура - flow of Amur

канал глубиноя 3-5 м - channel 3-5 m in depth
зона А - zone A, зона Б - zone B, зона В - zone V
бухта - bay

usually appears again at the surface 15–20 m from the cape (zone B), after which, sometimes remaining on the surface, it floated downstream passively for 50–100 m (zone V). An active movement of the animals upstream into zone "A" completes the "cycle". In some cases the animals accomplished some or other part of this "cycle", coming calmly to the surface several times (4–9) for periods of 1–7 s. Not even once were we able to observe the first slow movement on the traverse of the cape in a direction opposite to the shore.

The greatest average time of an animal staying on the surface of the water (average duration of "ventilation") was recorded in zone "B" (27.0 s). In zone "A" it comprised 23.0 s, while in zone "B" it was 15.0 s. The comparatively shorter average duration of the "ventilation" in zone "B" may apparently be explained by its closeness to the shore. The usual frequency of exhalations and inhalations during the "ventilation" comprised 1 in 2 s.

The "pursuit "stage. Having chosen a favourable moment, the spotted seal begins to pursue fish that are moving against the flow of the river. The tactics of the animal consist of "cutting corners", moving along the shortest path as the fish attempts to escape to the side. As a consequence of this, the trajectory of the seal's movements as a whole quite often had a zig-zag-like character. The usual length of a spurt in pursuit of a fish comprised 5–25 m at a speed of 3-4 m / s. Most spurts (56.3%) were noted in zone "A"; in zone "B" there were 25.4% and in zone "V" – 18.3%.

Stage of capture of the fish. In most case the spotted seal apparently catches the fish from below, by the belly, which is indicated by the numerous cases of fish found in the nets with laceration wounds in the belly region. Out of 71 recorded spurts of seals in pursuit of fish, 18 of these (25.4%) had a successful outcome.

In this season there were also recorded some characteristics of the behaviour of the spotted seal on the surface of the water (M. N. Shchekotov, 1986), which may be associated both with sexual behaviour (J. C. Beier and D. Wartzok, 1979) and are also components of play behaviour.

1. Synchronous dives of partners. When breathing on the surface, animals that form a pair remain not far from one another, at a distance of 1-2 m. However, if one of the partners appears on the surface of the water at some distance from the other (10–20 m), it looked around and, having found the other animal, it moved vigorously towards it on the surface, not losing it from sight. When one of the partners dived, the other, possibly the male, quickly dived after it.

2. "Pursuit". When the animals are submerged in the water in approximately half of the cases the pursuit of one seal by another was observed. The movements of partners abounded in sharp turns at high speed, and not infrequently the animals turned "on a dime"[8]. The duration of this type of behaviour comprised some tens of seconds, after which the animals dived.

3. "Saddling". In some cases during the pursuit the pursuing partner finds itself on top of the other animal and in this case both of the seals, moving at the surface, were able to swim several meters in this fashion.

4. Nasal contacts. The partners are positioned one opposite the other ("nose to nose") and touch one another with their forwardly directed vibrissae. The duration of this posture is 1–5 s. This behavioural element , which is widely distributed among pinnipeds, may be a constituent of some sequences of behavioural elements, including the "pursuit" of the animals and the "saddling".

b. Sound signals

The auditory and spectral analysis that was carried out on the material collected, pertaining to the underwater acoustic activity of the Amur spotted seal, made it possible to reveal about 1.5 thousand signals and to classify them into nine principal classes.

The relative share of the recorded signals of each class and the number of signals that were spectrally analyzed are presented in Table 14.

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[8] The Russian idiom is "on a handkerchief". [Tr.]

Table 14

Principal classes of the acoustical activity of the Amur spotted seal (July–October 1980 and 1983)

Name of class	Number of signals	% of total number of signals	Number of signals spectrally analyzed
1. "Single pulsed signal"	533	35.6	73
2. "Double pulsed signal"	222	14.8	42
3. "Short series of pulses"	96	6.4	18
4. "Long series of pulses"	143	9.6	16
5. "Champing"	211	14.1	29
6. "Ua", "Uo"	191	12.7	49
7. "Squeak"	35	2.3	6
8. "U", "Uk"	60	4.0	10
9. Other	8	0.5	-
Total	1499	100	243

Frequency-temporal characteristics of the principal classes of acoustic signals of the Amur spotted seal.

1. "Single pulsed signal". Duration of pulses varies from 0.005 to 0.05 s. The dominant frequency of most signals falls in the frequency band of 0.2–2.0 kHz. Frequency range of most of the pulses 0.2–8.0 kHz, in some signals above 16 kHz.

2. "Double pulsed signal". Total duration of signal 0.03–0.095 s. Duration of first pulse 0.005 to 0.025 s, of second pulse — 0.005–0.03 s. Interval between pulses 0.005–0.04 s. Dominant frequency of signals 0.2–1.5 kHz. Frequency range 0.2–9 kHz, in some signals – more than 16 kHz.

3. "Short series of pulses". Series of pulses (3–6) with a duration of 0.06–0.28 s and a repetition rate of 18–63 pulses per second. The duration of the individual pulses is 0.006–0.045 s, while that of the interval between pulses is 0.005–0.045 s. Dominant frequency 0.2–1.0 kHz. Frequency range — 0.2–6 kHz, of some series — up to 12 kHz.

4. "Long series of pulses". Numerous (7–26), more prolonged, longer than 1 s, series of pulses with a repetition rate of 14–56 pulses per second. Duration of individual pulses — 0.005–0.015 s. The dominant frequency of the majority of impulses falls in the frequency band of 0.2–1.0 kHz. The frequency range of the signals is 0.2–7 kHz, in some series — up to 12 kHz. The series may be made up both of pulses that are approximately uniform in their frequency-temporal characteristics, with almost equal intervals between the pulses, as well as of heterogeneous pulses with varying intervals between the pulses.

5. "Champing". Series of single or double pulses (2–7), with a duration of 0.17–0.96 s, with a repetition rate of the single or double pulses of 4 to 12 pulses per second. Duration of individual pulses — 0.005–0.04 s, duration of interval between them — 0.07–0.24 s. Dominant frequency of pulses in the following frequency intervals: 0.4–1.0 kHz (47% of total number of pulses); 1.1–2.6 kHz (32.0%); 0.8–1.6 kHz (13.6%); 1.1–3.5 kHz (4.9%); 2.4–3.8 kHz (2.9%) and 4.2–5.6 kHz (1.0%). In the elements of the series made up of two pulses the first pulse is expressed considerably more weakly with the major part of its energy at 0.2–0.5 kHz. The maximal value of the dominant frequency in the series made up of three elements is found in the second element, while in series with a different number of elements it occurs with no evident pattern of regularity, in elements of any ordinal number. The regions with the major part of the energy in neighbouring elements, as a rule, differ very considerably, by 0.3–1.2 kHz, and only in some cases may two or three successive elements have approximately the same values of the dominant frequency. Frequency range of series – 0.2–7 kHz, in several cases – more than 16 kHz.

6. "Ua", "Uo". Signals with a duration of 0.025–0.085 s, composed of 2–5 closely following pulses, which sometimes merge together. Interval between pulses — 0.005–0.025 s. Duration of individual impulses — 0.005–0.02 s. The region of the major part of the energy in the second half of the signal occupies a band of higher frequencies, by 0.3–0.6 kHz, than in the first half. From this also arises the effect of the auditory perception of the two sounds "u - a". In the first part of the signals the dominant frequency occurs in the

following frequency intervals: 0.2–0.5 kHz (9.6% of the total number of signals): 0.2–0.8 kHz (65.4%); 0.5–1.1 kHz (25%); and in the second part—into the following: 0.5–1.0 (34.1%); 0.8–1.6 kHz (48.9%); 1.4–2.3 kHz (14.9%); 1.3–3.1 kHz (2.1%). The frequency range of the signals is 0.2–6.0 kHz, in some cases – up to 8 kHz.

7. "Squeak". Short series (0.1–0.17 s), composed of 4–6 pulses, with a duration of 0.005–0.008 s , repeated at a high rate (56–100 pulses per second), with a following, after an interval (0.02–0.055 s), more powerful concluding pulse, with a duration of 0.01–0.02 s. The major part of the energy of the pulses in the first part of the signal is concentrated in the frequency intervals of 0.3–0.8 kHz and 0.6–1.1 kHz, while that of the concluding pulse — 0.2–1.8 kHz and 0.5–2.6 kHz. Frequency range of signals — 0.2–6 kHz, in several cases – up to 13 kHz.

8. "U", "Uk". For the most part single, rarely double with an interval of 0.015–0.04 s, signals with a duration of 0.03–0.22 s, made up of two and more almost merging pulses. Duration of pulses 0.005–0.02 s. The regions of the dominant frequencies of the signals are 0.2–0.4 kHz, 0.4–0.7 kHz and 0.6–1.0 kHz. In the second part of the signals may be found a decrease of the dominant frequency by 0.1–0.2 kHz. The frequency range of the signals is 0.2–4 kHz, in some cases – up to 7 kHz.

c. Acoustic activity

For analysis were selected 117 signal sequences of the Amur spotted seal, which did not overlap other sequences. The numbers of recorded sequences of the acoustic signals and the relative share of all classes of signals in sequences of different duration and with different numbers of signals are presented in Table 15.

The numbers of the principal classes of signals of the Amur spotted seal in the sequences with different numbers of signals and their relative shares are presented in Table 16.

Table 15

Character of the production of acoustic signals by the Amur spotted seal in Situation VI

Number of signals in sequences	Number of sequences of a given type	% of total number of sequences	Number of signals in sequences of a given type	% of total number of signals
1–4	29	24.8	82	6.2
5–10	40	34.2	253	19.3
more than 10	48	41.0	979	74.5
Total	117	100	1314	100
Duration of sequences (s)				
1–15, av. 6.8	67	57.3	359	27.3
16–30, av. 18.2	26	22.2	282	21.5
31–233, av. 52.9	24	20.5	673	51.2
Total:	117	100	1314	100

Table 16

Relative share of the acoustic signals of the Amur spotted seal in sequences with different numbers of signals (Situation VI, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Numbers of signals in sequences: 1–4		5–10		more than 10		Total signals	%
	P	%	P	%	P	%		
1. "Single pulsed signal"	37	45.1	90	35.6	318	32.5	445	33.9
2. "Double pulsed signal"	11	13.4	41	16.2	116	11.8	168	12.8
3. "Short series of pulses"	4	4.9	18	7.1	80	8.2	102	7.8
4. "Long series of pulses"	8	9.8	23	9.1	101	10.3	132	10.1
5. "Champing"	2	2.4	27	10.7	165	16.9	194	14.7
6. "Ua", "Uo"	8	9.8	42	16.6	142	14.5	192	14.6
7. "Squeak"	5	6.1	9	3.5	31	3.2	45	3.4
8. "U", "Uk"	7	8.5	3	1.2	21	2.1	31	2.3
9. Other	0	0	0	0	5	0.5	5	0.4
Total	82	100	253	100	979	100	1314	100

Table 17

Relative share of the principal classes of signals in sequences of different duration of the Amur spotted seal (Situation VI, P - number of signals of a given class; % - percentage of total number of signals)

Name of class	Duration of sequences (s)					
	1–15		16–30		33–98	
	P	%	P	%	P	%
1. "Single pulsed signal"	126	35.1	113	40.1	206	30.6
2. "Double pulsed signal"	50	14.0	46	16.3	72	10.7
3. "Short series of pulses"	30	8.4	19	6.7	53	7.8
4. "Long series of pulses"	41	11.4	22	7.8	69	10.3
5. "Champing"	31	8.6	24	8.5	139	20.7
6. "Ua", "Uo"	55	15.3	41	14.5	96	14.3
7. "Squeak"	13	3.6	9	3.2	23	3.4
8. "U", "Uk"	13	3.6	3	1.1	15	2.2
9. Others	0	0	5	1.8	0	0
Total	359	100	282	100	673	100

The numbers of the principal classes of signals, encountered in sequences of different duration, and their relative share are presented in Table 17.

From the material presented above it may be noted that in the Amur spotted seal signals of classes No. 1, No. 5, No. 2 and No. 6 comprise 77% of the total number of signals, and 50.4% of these are signals of classes No. 1 and No. 2 (Table 14).

As can be seen from Table 15, the Amur spotted seal produces only 25.5% of all of its signals in the form of short sequences (of 1–10 signals), and 74.5%—in the form of sequences with a number of signals greater than 10. The relative share of the short sequences (1–10 signals) comprises 59%, while the sequences with a larger number of signals comprise 41%.

In the groups of sequences, commencing with the first (1–4 signals) and ending with the last (more than 10 signals) there occurs a successive decrease in the relative share of the signals of the No. 1 and No. 2 classes from 58.5% to 44.3%, accompanied by an increase in the total percentage of the signals of classes No. 3, No. 4, No. 5 and No. 6 from 26.9 to 49.9% (Table 16).

The repetition rate of all classes of signals in the sequences of acoustic signals with a duration of 1–15 s is 51.2 signals per minute, and it decreases somewhat in the sequences of longer duration to 38 signals per minute.

As we can see from Table 17, the relative shares of the signals of almost all the classes in the acoustic signal sequences of the Amur spotted seal, which are of differing duration, change only slightly and only the share of the No. 5 class of signals increases with an increase in the duration of the sequences.

* * *

In spite of the fact that the two examined sections of the distribution range of the Far-Eastern spotted seal are located at a distance of more than a thousand km from one another, the characteristics of the underwater acoustical activity of the Kamchatka and the Amur spotted seals are very similar. This concerns not only the frequency and temporal characteristics of the principal classes of signals, but also the percentage ratios of each class of signals in the repertoire of the two populations. The greatest differences are noted for classes No. 2, No. 3, No. 4 and No. 5. The share of the No. 5 class of signals is 3.9 times as high in the Amur spotted seal (Tables 1 and 14), while, on the other hand, the share of the signals belonging to classes No. 2, No. 3 and No. 4 is 1.5–2.0 times higher in the Kamchatka spotted seal. The indicated differences, in our opinion, may be associated primarily with the ecological features of the specific habitats, which determine the particular character of the searching and hunting behaviour and the social behaviour of the animals.

The overwhelming majority of the signals of the Amur spotted seal are produced in the form of sequences with a number of signals greater than 10 (Table 15), the percentage of which is very considerable (41%). A similar pattern is found also in Situation IV in the Kamchatka spotted seal (Table 9). The situation is somewhat different in Situations I, II and III, where the percentage of sequences with a number of signals greater than 10 is markedly smaller (15–17%, Tables 2, 4 and 6), while the relative share of the signals produced in the form of this type of sequences is equal to only 48–53%.

If one speaks of the duration of sequences, then also found to be higher in the Kamchatka spotted seal are the average duration (Tables 9 and 15) and the percentage of sequences with a duration greater than 30 s (more than 3 times as high, in comparison with the Amur spotted seal), although in the Kamchatka spotted seal the repetition rate of the signals in the sequences is somewhat lower.

Considering the situations in which the recordings of the acoustic activity of the Far-Eastern spotted seal were carried out, one may divide them into two groups: the situations in which the presence of man affected the behaviour and, consequently, also the acoustical signalization of the seals (I, II, III and V), and the situations in which the effect of man was minimal (IV and VI). The presence of the anthropogenic factor, as an external danger to the animals in the first instance, in our opinion, should depress those aspects of the signalization that are connected with different forms of social behaviour. Thus, our observations in the coastal zone of the Amur liman (Situation VI) show that the pursuits, "saddlings", nasal contacts and other displays of the social activity of the animals immediately came to a stop with the appearance of man, coming out of a hiding place. It is logical to assume that in cases of this type it is more important for the animal to have information on the positioning of a dangerous object, which may be obtained under the water by the use of sonar direction finding or else by series of echolocation signals.

Furthermore, in Situation IV, the particular level of social contacts that was displayed on the on-shore hauling-out grounds of the seals provides a basis for assuming that the social activity is also continued in the water, all the more so since the "howl" and "growling", that are common to the animals in air, have been recorded by us also in the water.

Thus, we are dealing here with situations of two kinds: those in which the forms of social behaviour have been reduced to a minimum as a result of present danger and, in the case where the danger factor is at work for a sufficiently long time and is not intensified, there occurs a restoration of the searching and hunting activity — as in Situations I, II, III and V; and those in which the normal social behaviour of the animals is found — as in Situations IV and VI.

Let us consider how the acoustical signalization of the spotted seal changes depending on the situation. To this end, on the basis of the available literature data, we will combine the principal classes of signals into three groups. In the first group are included the signals of classes No. 1 and No. 2 (single and double pulses). In oceanarium conditions American investigators have obtained data on the utilization by the common seal (closely related to the spotted seal) of single and double pulses for purposes of echolocation (D. Renouf and M. B. Davis, 1982). The temporal and frequency characteristics of the pulses obtained by us for the spotted seal were found to be very similar to the signals of the common seal. Thus, one may assume an echolocation function of the signals of classes No. 1 and No. 2.

In the second group may be included the remaining classes of signals, which are used for purposes of communication and purposes of social behaviour. As studies on the spotted seal in an oceanarium have shown, series of pulses may be produced by both males and females, and they are very common during courting and mating (J. C. Beier and D. Wartzok, 1979), which has also been corroborated by data obtained in free-living conditions (D. Wartzok et al., 1981, as cited in D. Wartzok et al., 1984). In the common seal signals of this kind have been noted in conditions of captivity during aggressive encounters (R. J. Schusterman et al., 1970).

Other classes of signals, associated with breeding behaviour, include growling, chirping, barking and squeaking (J. C. Beier and D. Wartzok, 1979).

In Table 18 are presented the relative shares of these two groups of signals in different situations.

Table 18

Acoustical signalization of the Far-Eastern spotted seal in situations I–VI

Situation	Nos. of classes of signals	
	No. 1 - No. 2 (echolocational)	No. 3 - No. 9 (communicative–emotional)
I	77.6%	22.4%
II	80.8%	19.2%
III	76.6%	23.4%
V	86.3%	13.7%
IV	50.8%	49.2%
VI	50.4%	49.6%

Table 19

Character of the production of acoustic signals by the Far-Eastern spotted seal in situations I–VI

Situation	% of sequences with number of signals 1–10	% of sequences with number of signals greater than 10	% of signals of all classes in sequences (1-10 signals)	% of signals of all classes in sequences (more than 10 signals)
I	84.6	15.4	51.1	48.9
II	82.7	17.3	46.9	53.1
III	82.8	17.2	49.7	50.3
V	90.9	9.1	60.9	39.1
IV	15.5	84.5	3.9	96.1
VI	59.0	41.0	24.0	76.0

As can be seen from Table 18, in Situations I–III and V, as compared with Situations IV and VI, a high percentage of echolocational signals is recorded and a lower (by a factor of 2.1–3.6) relative share of signals used for purposes of social behaviour. Thus, one finds a very considerable degree of correspondence of the data obtained in the oceanarium conditions and in the conditions of the natural habitat.

Depending on the situation, changes also occur in the character of the acoustic signals produced by the spotted seal: in situations I–III and V the percentage of short (with 1–10 signals) sequences increases by 1.4–5.9 times, and the relative share of the sequences with a number of signals greater than 10 decreases by a factor of 2.4–9.3 (Table 19).

Thus, the characteristics of the underwater acoustical signalization of the Kamchatka and Amur spotted seal are very similar. The effect of the anthropogenic factor depresses the social behaviour of the animals and, in particular, certain aspects of the signalization. Becoming predominant in these cases are the classes of signals which are apparently used by the animals for purposes of echolocation. As this takes place there is also noted a sharp decrease in the number of signals in the sequences, which is evidently associated with the abbreviation in the time of social interactions of the seals.

2. The searching and hunting behaviour and the signalization of the Kamchatka spotted seal in the "river-sea" system

Repeated studies on the behaviour and acoustical activity of the Kamchatka spotted seal in the Ozernaya river were carried out by us in September–October 1986. At this time the quantity of the salmon run (char, coho) had already decreased considerably in comparison with the summer months. Another difference of this season of work is the comparatively large number of seals that move into the river: usually 10–14 individuals, sometimes up to 40 individuals. Furthermore, for the first time observations were carried out from a "high-rise" observation point — the "tower" (Figure 10), situated at a height of about 15 m above the water level in the river, which, in the presence of favourable conditions (clear weather, absence of wind, high transparency of the water, etc.) , allowed us to note characteristics of the underwater behaviour of the spotted seal in synchrony with the recording of the acoustical activity.

a. Dynamics of hunting activity

The presence of seals in the river, their behaviour and their underwater acoustical activity in the region of observation are determined by several factors: the intensity of the fish run during the rising tide and the ebb tide, the degree of the anthropogenic effect on the animals, the velocity of flow of the river during the rising and ebbing tide, the state of the surface of the sea, etc. The main food objects of the spotted seal during the period of the observations are the char and coho, which move up the river, predominantly during the rising tide, to a considerably smaller degree during high ebb tide (incomplete low tide) and practically do not enter the river at all during the low ebb tide (full low tide). As a result of this the maximal number of animals in the river is found over the course of the 2–3 hours prior to and following the passage of the highest point of the high tide, although most of the seals may remain in the river also during the high ebb tide, in the absence of factors of an anthropogenic effect. This leads to the situation that the average number of animals in the river recorded at this time is decreased by only a factor of 1.4 from that found during the high tide. At the time of the low ebb tide the absence of fish and the intensified effect of the current of the river forces most of the seals to move out into the sea.

Searching and hunting behaviour of the seals is observed practically all the time, when at least some individual salmon (during the high ebb tide) move upstream (Table 20; here and subsequently the index "High tide +4+3" denotes a time 3–4 hours prior to the passage of the highest point of the high tide, and correspondingly "High tide -1-3" — one-three hours after the highest point, and similarly for the other indices).

Table 20

Level of hunting activity of the Kamchatka spotted seal during the rising and ebbing tide.

Time of high and low tide	High tide			High ebb tide
	+4+3	+2+0	-1-3	+3+1
Calculated number of spurts (spurts / hr / individual)	0.4–3.2 av. 1.4	0.7–1.9 av. 1.0	0.8–2.2 av. 1.2	0.4–1.9 av. 0.8
Success of spurts	50.0%	47.8%	77.6%	57.1%
Time of observations (hr)	4.0	8.0	7.3	7.0

b. Searching and hunting behaviour

The searching and hunting behaviour of the spotted seal includes the searching and waiting behaviour of the seals under water — the "patrolling", which may be observed, when the water is highly transparent, beside the wall of the pier, as well as, from the "tower", in the area of water near the shore in the river. This comprised the following behaviour. Having completed a series of inhalations and exhalations, the animal moved down from the surface under the water (edge of zone V, Figure 10) and began to swim slowly in the direction towards the wall of the pier, at a depth of about 2 m, sometimes along a complex looping trajectory (Figure 10). Frequently, as this takes place, the body of the animal was inclined in such a way that the anterior part and the head were positioned below the posterior part of the body. The seal approached the wall of the pier and either began slowly "patrolling" along it or came to a halt in "ambush" (Figure 10). The position of the body of the animal in "ambush" in relation to the mouth of the river is probably determined by the force and direction of movement of the water in the river. During the rising tide the current of the river itself is weakly expressed and, although the seals are oriented at some angle, they nevertheless have their head towards the mouth of the river. The intensifying flow of the river during the ebb tide leads to the situation that the animals in "ambush" were oriented with their head in a direction opposite to the mouth of the river. In this case the specific inclined posture, in which the anterior part of the body is positioned somewhat below the posterior part, is frequently retained.

On discovering a fish, the spotted seal made a headlong spurt and, as this takes place, the nearest 2-3 seals immediately joined in the pursuit. In the course of the observations from the tower we established, for the first time, that in 60–80% of the cases 2–4 animals simultaneously participate in the spurts in pursuit of a fish (Figure 11). There is, apparently, a certain distance (about 10–15 m) at which "neighbours" join up in the pursuit. Thus, on several occasions we have observed that animals at a greater distance

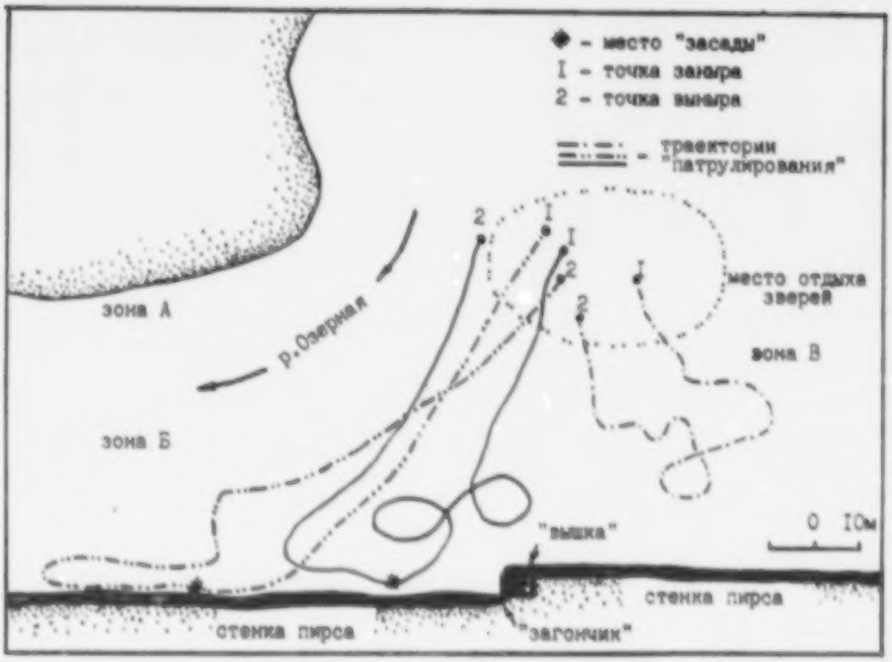
◆ - место "засады"
I - точка заныра
2 - точка выныра
- траектории "патрулирования"
место отдыха зверей
зона А
зона Б
зона В
р. Озерная
"вышка"
стенка пирса
"загончик"
0 I0м
I
2

Рис.I0.Траектории "патрулирования" камчатской ларги (р. Озерная,сентябрь 1986 г.)

Figure 10. Trajectories of "patrolling" behaviour of Kamchatka spotted seals (Ozernaya river, September 1986)

* - place of "ambush"
1 - point of submergence
2 - point of coming to the surface

— · — · —, – ·· – ·· –, ———— - "patrolling" trajectories

◌ место отдыха зверей - resting location of animals

зона А, зона Б, зона В	–	zone A, zone B, zone V
← р. Озерная ←	–	← Ozernaya river ←
"вышка"	–	"tower"
стенка пирса	–	wall of pier
"загончик"	–	"pen"

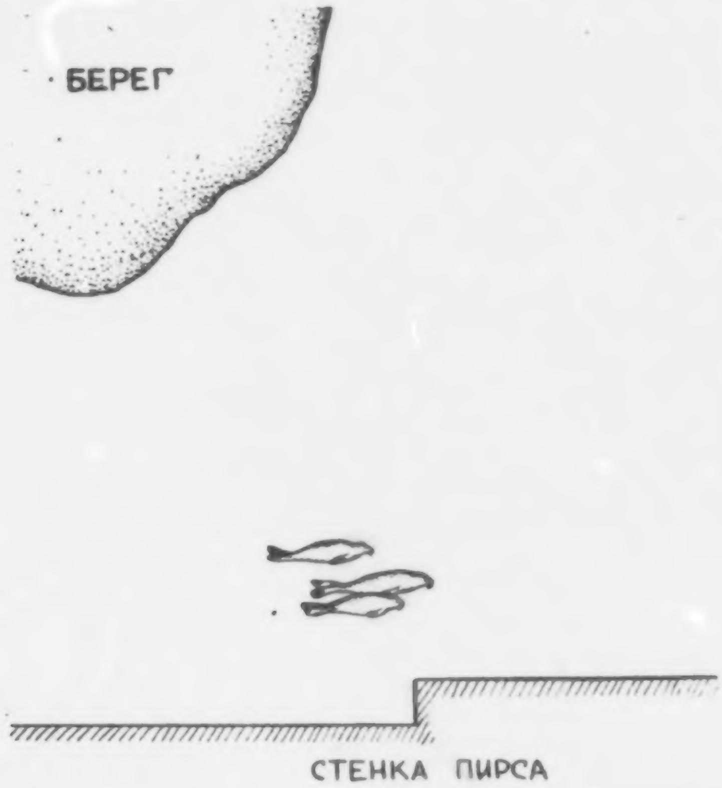

Рис.II.Групповой бросок камчатской ларги за рыбой (р. Озерная).

Figure 11. Group spurt of Kamchatka spotted seal in pursuit of a fish (Ozernaya river).

БЕРЕГ - SHORE
СТЕНКА ПИРСА - WALL OF PIER

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reacted to the onset of a hunt only by turning towards the hunting seals but at the same time they remained in their place. Furthermore, according to our observations, animals that were on the surface joined up in the pursuit at a markedly later time than those that were under the water at that moment.

The movements of the animals during the spurt is extremely diverse and may occur in the position of the animal on its back and on its side (Figure 12). Apparently, on account of the drastic restriction of the possibilities for manœuvering for the prey, the probability of a successful hunt in the case of such "collective" spurts is very high. Unsuccessful spurts were observed by us in only 5–10 % of the cases.

Aggressive and competitive relations between the seals are usual for such group spurts. Quite often the skirmishes that arise at the end of the hunt, including energetic movements of the fore flippers and bites, lead to the fish getting to the largest and the strongest animal, even in those cases when it was initially caught by another individual. More prolonged and bitter skirmishes on account of the catch, accompanied by pursuits and energetic movements of the fore flippers occur when there is a clash of rivals that are approximately equal in strength and hierarchical position, and in this case they may emit specific acoustic signals (see below).

Рис.12.Положение тела камчатской ларги во время броска
(р. Озерная, октябрь 1986 г.).

Figure 12. Body position of a Kamchatka spotted seal during a spurt
(Ozernaya river, October 1986).

The fish may be devoured either at the surface or under water. When the fish is devoured under water the animal executes distinct swallowing movements with the anterior part of its body. Swallowing commences with the head of the fish and with each such movement the prey disappears deeper and deeper into the mouth of the animal.

The consumption of the fish on the surface may vary in its character. The young animal swallows the fish in a hurry; the seal, as it were, expects to be attacked. The process lasts for about half a minute or a little more. A large animal of high rank consumes its prey in a somewhat demonstrative manner, especially in those cases when it is no longer hungry. Such an animal may even abandon the fish, pursue another animal and then once more take up its prey, or else pursue another individual without releasing the fish from its mouth. With the fish in its mouth it may produce characteristic acoustic signals, which are associated with demonstration behaviour above the water (Table 29, Figure 17). The swallowing process is stretched out for up to 2–5 minutes. In rare cases, during an encounter, two seals, seizing hold of one fish at the same time, may tear it apart into two parts, and then each animal swallows its own share.

The pursuit and consumption of the fish may also take place on land, if the fish leaps out onto the shore as it is being chased. The seal comes out after it onto the shore and swallows it, as usual, head first, sometimes executing in the process swallowing movements similar to those which are performed under water.

The parts of the water area of the river are apparently not at all of equal value from the point of view of the success of the hunt. The seals very effectively made use of the wall of the pier as a barrier against which it was convenient to pin down the pursued fish (Table 21, Figure 10).

Table 21

Hunting success of the Kamchatka spotted seal
on different parts of the water area of the river

Parts of the water area	Wall of pier	Zone "A"	Zone "B"	Zone "V"
Hunting success	84.9%	31.0%	48.1%	61.1%
% spurts of total number of spurts (228)	40.8%	12.7%	22.8%	23.7%

The fish had the least opportunity to evade its pursuers in the "pen" that was formed by the walls of the pier (Figure 10). The distribution of animals of various size and age was also found not to be uniform. Beside the wall of the pier, which was the most propitious section of this area of water for hunting, there were predominantly found large individuals, which apparently held a high hierarchical position. Only sporadically were pursuing spurts by small animals observed in this section, while large animals rarely stayed and hunted in the "A" and "B" zones, which show little promise. A large animal, "patrolling" the section beside the wall of the pier, chased away others that were in the vicinity, quite often making use of acoustic signals and blows with the fore flippers for this purpose.

It was found that the success rate of fish captures by the large adult animals was 1.7–1.9 times greater than that of the small young animals. It is possible that this is associated with the predominant utilization by the young animals of a special type of searching and hunting behaviour. The small seals, distributed in an ordered manner at a small distance from one another in the shallow water (zone "V"), created a sort of trap "net", the distance between the individual animals of which was approximately uniform (5–10 m, Figure 13A). The number of seals making up such a net varied form 4 to 35, depending on the external factors. Depending on these numbers, the width and also, obviously, the fishing efficiency of such a "net" varied. With large numbers, the animals arranged themselves in a staggered order into two and sometimes even into three rows. A fish that fell into the "net" was immediately pursued by 3-4 neighbouring spotted seals, which drastically restricted the possibilities for manœuvering of the prey. As we have already mentioned, failure was rarely observed in the group spurts (5–10%). In this way, the "net" increases the probability of a fish catch also for the young seals. The large animals which are located beside the wall of the pier and in the channel of the river between zones "A" and "B" may in this case fill the roles of passive and active "beaters", herding the fish, that were moving upstream, into the "net". This kind of "net", probably made up of individuals of various age, was also found by us in the sea and in areas in front of estuaries.

It should be noted that, on the whole, the searching and hunting behaviour of the spotted seal in the Ozernaya river has a dynamic character and is well adapted to the changing external conditions. The number of animals in a group also has no small effect on the tactical methods used in the hunt. The above-described system of "control" and following one another in the seals under water and, resulting from this, the possibility for combined spurts may lead, especially in small groups (of 4–6 individuals), to a type of searching and hunting behaviour in which the majority of the seals strive to appear on the surface together and are found under water for most of the time also together. According to our data, the time during which most of the animals of such groups appeared on the

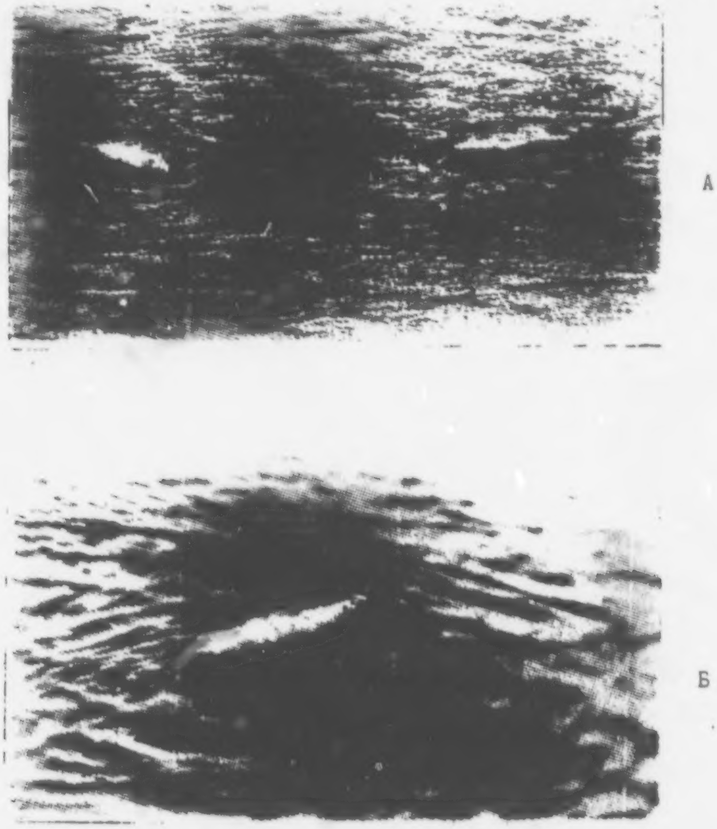

Рис.13.Поведение камчатской ларги: А – участок "сети", образованной молодыми животными; Б – крупный светлый зверь на поверхности.

Figure 13. Behaviour of the Kamchatka spotted seal:

А - A - portion of "net" formed by young animals;

Б - B - large light-coloured animal on the surface.

surface was 3–50 s, average 17.8 s, while the time from the appearance of the last animal on the surface to the submersion of the last individual was 10–43 s, average 34.2 s. The time during which all of the animals were under water varied from 26 to 303 s, with an average of 149.2 s.

Observations from the tower on an animal that had a natural marker, a very light coloration of its pelt (Figure 13B), allowed us to obtains some data on the time of breathing on the surface and the duration of the respiratory pauses. For this large light-coloured animal the times of staying underwater comprised 0.7–7.0 min, average 3.5 min, while the duration of breathing on the surface was 30–45 s, average 39.1 s. By and large, the duration of breathing, according to observations on other animals, comprised 5–22, average 12.4 inhalations-exhalations. It is interesting to note that the most preferred location for coming to the surface, breathing and resting of the spotted seal on the surface was a shallow-water area with a more tranquil flow of the river (edge of zone "V", Figure 10), to a lesser degree zone "B" and the channel of the river between zones "A" and "B". The animals practically did not appear at all on the surface close to the wall of the pier, which was probably associated with the presence of man.

c. Acoustic signals

The searching and hunting activity, the predominant type of behaviour of the spotted seal in the region of the observations, was accompanied by a large number of sound signals.

The spectral-temporal and auditory analysis of the collected material on the underwater acoustic activity of the Kamchatka spotted seal allowed us to reveal more than 27 thousand signals and to classify them into thirteen principal classes (Table 22).

From the table it follows that more than 84% of all the signals comprise signals of the following four classes: No. 2, No. 1, No. 6 and No. 5. The summed percentage of the first two classes comprises 66.9%.

Some frequency-temporal characteristics of the signals of the principal classes of the spotted seal were presented in the previous chapter and therefore we will give here a description only of the more rarely encountered classes of signals:

9. "Bleating". Duration of signals— 0.47–0.66 s. The signals make up series, consisting of 5–7 pulsed bursts, with a duration of 0.03–0.09 s; in each with 2–7 pulses which merge together. Dominant frequency— 0.2–1.3 kHz. Frequency range of signals — 0.2–1.5 kHz (Figure 14A).

Table 22

Principal classes of acoustic signals of the Kamchatka spotted seal (September–October 1986, Ozernaya river))

Name of class	Number of signals	% of total number of signals
1. "Single pulsed signal"	6591	24.0
2. "Double pulsed signal"	11768	42.9
3. "Short series of pulses"	803	2.9
4. "Long series of pulses"	1101	4.0
5. "Champing"	1795	6.5
6. "Ua", "uo"	3040	11.1
7. "Squeak"	957	3.5
8. "U", "Uk"	278	1.0
9. "Bleating"	322	1.2
10. "Howl"	282	1.0
11. "Uaa"	180	0.7
12. "Ufkh"	173	0.6
13. Others	165	0.6
Total	27455	100

10. "Howl". The signals comprise long (0.42–3 s) series of pulses, with a repetition rate of 80–150 pulses/s. Dominant frequency — 0.2–0.6 kHz and 0.9–1.4 kHz. Frequency range of the signals — 0.2–3.0 kHz. It is possible that these signals are emitted in air and pass into the water through the body of the half submerged animal.

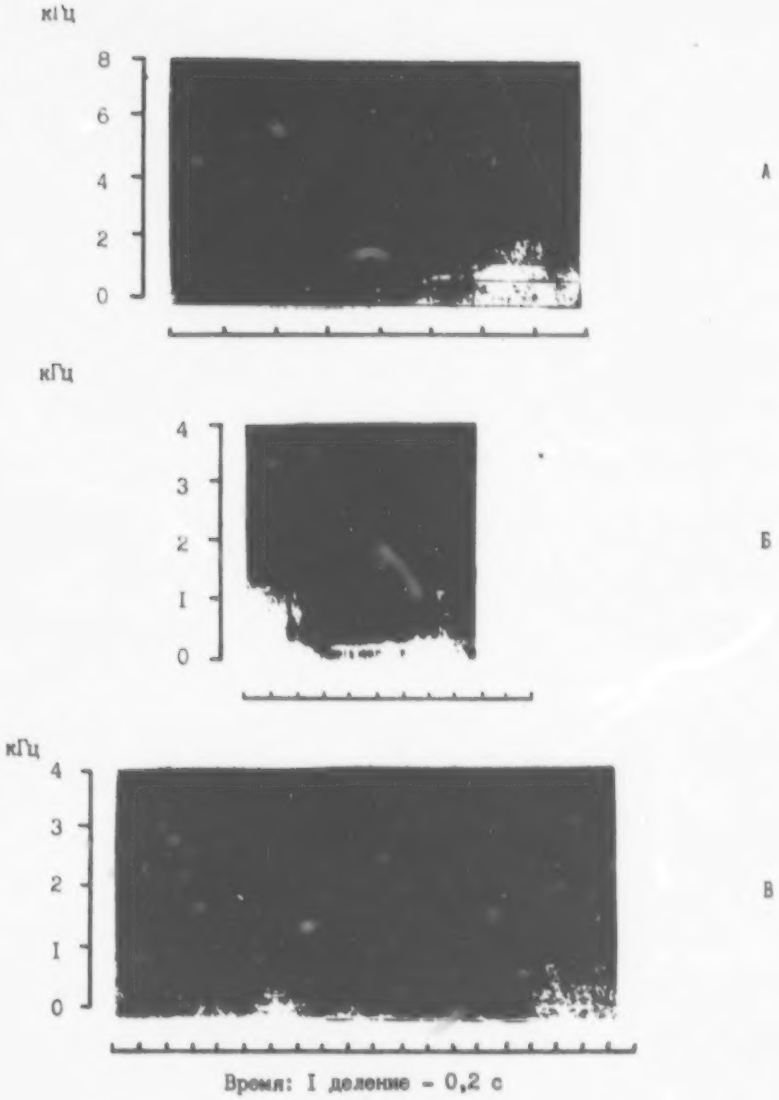

Рис. I4. Звуковые сигналы ларги основных классов:
А) № 9; Б) № II; В) № I2

Figure 14. Principal classes of sound signals of the spotted seal:
А - A) No. 9; Б - B) No. 11; В - V) No. 12.
ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

11. "Uaa". Duration of signals — 0.87–1.05 s. Dominant frequency lying within the limits of 0.4–1.2 kHz. Frequency range of signals — 0.1–2.5 kHz (Figure 14 B).

12. " Ufkh". The signals (2–4) follow with pauses of 2-3 s. Duration of signal, made up of several merged pulses — 0.07–0.09 s. Dominant frequency 0.8–1.0 kHz. Frequency range of signals 0.3–2.0 kHz (Figure 14V).

d. Dynamics of sound activity

The level of the acoustical activity of the animals is determined by several factors, such as the state of the tide, the time of day, the degree of disturbance by man, etc. For a quantitative characterization of the effect of these factors it is necessary to consider the following features of the signalization of the spotted seal under water.

As we have already mentioned, the direct observations on the behaviour of the spotted seal under water with the simultaneous audio-monitoring of the area of water, as well as the data from the subsequent auditory analysis indicate that the signals are usually produced in the form of sequences by 1-2 individuals, and moreover the signals in each particular sequence have approximately the same intensity. The last signal in a sequence was considered to be the signal following which no signal was produced for a period of 30 s (this time interval is 10–26 times greater than the average interval between signals in various types of sequences).

On the basis of their qualitative composition we divided all of the signal sequences (SS[9]) into three types Included in the type "A" SS were the sequences that were made up only of the No. 1 class signals (single pulsed signals) or of the No. 2 class signals (double pulsed signals), or else of the one and the other. In 1982, data were obtained in oceanarium conditions, which provided evidence of the use by the common seal (closely related to the spotted seal) of single and double pulses for purposes of echolocation (D.

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[9] The Russian abbreviation is ПС (PS - posledovatel'nosti signalov – sequences of signals). [Tr.]

Renouf and M. B. Davis, 1982). The frequency-temporal characteristics of the pulses of the spotted seal, which were obtained by us, were found to be very similar to the signals of the common seal. Thus, an echolocation function may be assumed for the sequences of single and double pulses (type "A" SS) in the spotted seal.

In the type "B" SS are included sequences which contain signals of all classes in arbitrary combinations besides those indicated for the type "A" SS. Many of these classes (series of pulses of different duration, squeaks, signals resembling barking, etc.) have been noted in captivity during aggressive encounters in the common seal and in the spotted seal (R. J. Schusterman, 1970; J. C. Beier and D. Wartzok, 1979). By and large the type "B" SS may be formed both exclusively as communicative and emotional signals (signals of classes No. 3 - No. 13), as well as in combination of these classes with single and double pulses (classes No. 1 and No. 2).

In the type "V" SS are included the sequences of signals which are formed as a result of the superposition of sequences of the first two types, produced simultaneously in different points of the area of water in the region of the biological studies, as a consequence of which the intensity of the signals in them may differ considerably. The change in the level and character of the underwater acoustical activity of the spotted seal, depending on the tidal phenomena, the time of day and the degree of the anthropogenic effect, may be characterized by several parameters (Table 23).

As we can see from the Table, the indices of the frequency of occurrence of all the classes of signals, "signals / minute" and "signals / hour / individual", characterize the different situations in a similar fashion (Table 23, sections 1 and 2); from this point on we will consider only the values of the "signals / hour / individual" index.

From Table 23 it follows that the highest level of sound signalization of the Kamchatka spotted seal (57.8–78.3 signals / hour / individual) is noted during the night period, at high tide (sections 1 and 2). At this time the maximal values of the frequency of occurrence of the CES[10] classes No. 3 - No. 6 and No. 8 - No. 13 are associated with the highest frequency of occurrence of the type "B" SS, containing the signals of these classes and the highest comparative share of such sequences (Table 23, sections 2, 4, 5). The more extensive utilization by the Kamchatka spotted seal of the CES classes (No. 3 - No. 6 and No. 8 - No. 13) during the night, in the "high tide – norm" and "low ebb tide" situations (the share of these classes during the low ebb tide is 2.8 times greater at night than during the day) (Table 23, section 2) in comparison with the daylight period of the day may apparently be explained by the decrease in the degree of the anthropogenic factor during the night period. Besides this, it is possible that the animals feel themselves to be in greater security in the darkness and this increases the probability of any kinds of social contacts. An increase in the level of acoustical activity during the night hours has been noted also in the common seal (Renouf D. et al., 1980).

For the daylight hours, during the high tide it is interesting to underline the differing degree of decrease of the "signals/hour/individual" index for the different groups of signals: smaller—for the echolocation signals of classes No. 1 and No. 2 (by a factor of 1.5) in comparison with the night period; larger — for the communicative and emotional signals of classes No. 3 - No. 6 and No. 8 - No. 13 correspondingly by a factor of 2.7, and also the increase in the frequency of occurrence of the type "A" SS and of their relative share at this time (Table 23, sections 4–5).

The "low ebb tide" situation, both during the day and during the night, is characterized by a drastic decrease in the frequency of occurrence of all classes of signals as compared with the rising tide, which also varies for the groups of signals under consideration: of classes No. 1 + No. 2 by 5.6–5.8 times, of classes No. 3 - No. 6 and No. 8 - No. 13 by 10.1–10.3 times (Table 23, section 2), i.e. the drastic decrease in the level of acoustic activity observed during the low ebb tide, in comparison to the high tide, during the night and during the day, applies to a much greater degree to the CES classes. During the low ebb

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[10] The Russian abbreviation is КЭС (KES - kommunikativno-émotsional'nye signaly — communicative and emotional signals). [Tr.]

Table 23

Underwater acoustical activity of the Kamchatka spotted seal in relation to the tidal phenomena, the time of day and the degree of anthropogenic activity *

Number and name section in the table	Day								Night							
	High tide - norm			Low tide		High tide			High tide - norm			Low tide		High tide		
	+4+2	+1-1	-2-3	l.e.t. -2-3	h.e.t +2-1	S. No.1 +3+0	S. No. 2 +4-3	S. No. 3 +3-2	+4+2	+1-1	-2-5	l.e.t. +3+2	h.e.t ±0.5	S. No.1 +2-3	S. No. 2 +4+0	S. No 3 +4-4
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Frequency of occurrence of signals of all classes (sign / min)	5.2	9.0	7.2	1.1	5.2	0.5	3.1	5.5	9.9	11.2	14.1	3.4	1.2	2.1	0.3	4.6
2. Frequency of occurrence of signals of classes (signals / hour / individual)																
all classes	35.1	35.1	37.2	6.4	27.7	3.4	14.9	19.2	53.8	57.8	78.3	15.8	9.6	10.9	1.7	28.4
No. 1	7.5	6.4	7.5	0.9	6.6	1.0	1.2	3.9	12.5	13.9	22.7	4.0	2.8	1.5	0.3	6.4
No. 2	16.4	20.5	20.2	3.6	12.5	1.7	11.1	9.6	20.5	24.3	24.3	5.6	4.2	7.5	1.0	15.0
No. 3 + No. 4	1.8	1.2	1.2	0.1	1.9	0	0.3	0.3	5.6	4.5	8.4	1.1	0.4	0	0	1.1
No. 5	2.7	2.6	1.7	0.4	1.8	0.1	0.9	2.2	4.0	3.2	5.0	1.2	0.8	0.6	0	1.5
No. 6	3.6	1.7	3.5	0.2	3.1	0.8	0.1	1.2	7.0	7.3	12.1	1.9	0.4	0.5	0	1.5
No. 7	1.3	1.1	1.7	1.1	1.0	0.06	1.4	0.8	1.4	2.0	1.4	0.8	0.4	0.7	0.3	2.4
No. 8	0.4	0.3	0.2	0.05	0.13	0	0.04	0.03	0.9	0.7	1.6	0.09	0.03	0.3	0	0.07
No. 9 + No. 12	0.6	0.5	0.4	0	0.4	0.02	0	0.04	1.4	1.0	1.2	0.08	0.3	0	0	0.3
No. 10	0.16	0.07	0.04	0	0.06	0	0	0	0.19	1.1	0.7	0	0.2	0	0	0

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* S. No. 1 — situation No. 1 – presence of people on the shore, whose activity exerts a strong effect on the seals (catching fish, throwing stones, etc.); S. No. 2 — situation No. 2 – passage through the area of water of a vessel (MPC - MRS) [malyi rybolovnyi seiner - small fishing seiner] plus 3 minutes after this; S. No. 3 — situation No. 3 — 10 - 15 minutes after the termination of situation No. 2; the index "ОТЛИВ Н.М.В. -2-3" [translated here as "Low tide l.e.t. -2-3"], by analogy with the interpretation given in Table 26 [Sic. However a reference to Table 20 was probably intended. - Tr.], designates the time two to three hours after the passage of the point of the low ebb tide; the index "ОТЛИВ В.М.В. +2-1" [translated here as "Low tide h.e.t. +2-1"] designates the time interval from two hours before the point of high ebb tide to one hour after high ebb tide, etc.

Table 23

Underwater acoustical activity of the Kamchatka spotted seal in relation to the tidal phenomena, the time of day and the degree of anthropogenic activity *

Number and name section in the table	Day								Night							
	High tide - norm			Low tide		High tide			High tide - norm			Low tide		High tide		
	+4+2	+1-1	-2-3	l.e.t. -2-3	h.e.t +2-1	S. No.1 +3+0	S. No. 2 +4-3	S. No. 3 +3-2	+4+2	+1-1	-2-5	l.e.t. +3+2	h.e.t ±0.5	S. No.1 +2-3	S. No. 2 +4+0	S. No. 3 +4-4
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1. Frequency of occurrence of signals of all classes (sign / min)	5.2	9.0	7.2	1.1	5.2	0.5	3.1	5.5	9.9	11.2	14.1	3.4	1.2	2.1	0.3	4.6
2. Frequency of occurrence of signals of classes (signals / hour / individual)																
all classes	35.1	35.1	37.2	6.4	27.7	3.4	14.9	19.2	53.8	57.8	78.3	15.8	9.6	10.9	1.7	28.4
No. 1	7.5	6.4	7.5	0.9	6.6	1.0	1.2	3.9	12.5	13.9	22.7	4.0	2.8	1.5	0.3	6.4
No. 2	16.4	20.5	20.2	3.6	12.5	1.7	11.1	9.6	20.5	24.3	24.3	5.6	4.2	7.5	1.0	15.0
No. 3 + No. 4	1.8	1.2	1.2	0.1	1.9	0	0.3	0.3	5.6	4.5	8.4	1.1	0.4	0	0	1.1
No. 5	2.7	2.6	1.7	0.4	1.8	0.1	0.9	2.2	4.0	3.2	5.0	1.2	0.8	0.6	0	1.5
No. 6	3.6	1.7	3.5	0.2	3.1	0.8	0.1	1.2	7.0	7.3	12.1	1.9	0.4	0.5	0	1.5
No. 7	1.3	1.1	1.7	1.1	1.0	0.06	1.4	0.8	1.4	2.0	1.4	0.8	0.4	0.7	0.3	2.4
No. 8	0.4	0.3	0.2	0.05	0.13	0	0.04	0.03	0.9	0.7	1.6	0.09	0.03	0.3	0	0.07
No. 9 + No. 12	0.6	0.5	0.4	0	0.4	0.02	0	0.04	1.4	1.0	1.2	0.08	0.3	0	0	0.3
No. 10	0.16	0.07	0.04	0	0.06	0	0	0	0.19	1.1	0.7	0	0.2	0	0	0

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* S. No. 1 — situation No. 1 – presence of people on the shore, whose activity exerts a strong effect on the seals (catching fish, throwing stones, etc.); S. No. 2 — situation No. 2 – passage through the area of water of a vessel (МРС - MRS) [malyi rybolovnyi seiner - small fishing seiner] plus 3 minutes after this; S. No. 3 — situation No. 3 — 10 - 15 minutes after the termination of situation No. 2; the index "ОТЛИВ Н.М.В. -2-3" [translated here as "Low tide l.e.t. -2-3"], by analogy with the interpretation given in Table 26 [Sic. However a reference to Table 20 was probably intended. - Tr.], designates the time two to three hours after the passage of the point of the low ebb tide; the index "ОТЛИВ В.М.В. +2-1" [translated here as "Low tide h.e.t. +2-1"] designates the time interval from two hours before the point of high ebb tide to one hour after high ebb tide, etc.

Continuation of Table 23

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
3. % of signals of classes out of the total number of signals																
No. 1 and No. 2	68.7	76.6	74.5	70.4	68.0	82.5	75.6	70.1	61.2	66.1	61.1	61.3	60.8	81.9	80.0	74.8
All classes except No.1, No. 2 and No. 7	27.5	20.2	20.9	12.6	26.3	15.8	15.2	25.8	36.2	30.5	36.9	33.9	34.9	11.8	0	16.3
No. 7	3.8	3.2	4.6	17.0	5.7	1.7	9.2	4.1	2.6	3.5	2.0	4.8	4.2	6.3	20.0	8.8
4. Frequency of occurrence of sequences (SS / hour)																
of type A	12.0	18.6	22.2	-	12.6	7.7	13.2	15.6	10.8	11.4	12.6	15.6	5.4	5.5	6.0	15.0
of type B	13.2	5.4	9.6	-	10.2	0	4.8	13.2	18.0	10.8	15.0	8.4	3.6	2.8	0	8.4
of type V	2.4	2.4	1.8	-	1.2	0	0	0	3.6	3.6	4.2	0.6	0	0	0	0
of all types	27.6	26.4	33.6	-	23.9	7.7	18.0	28.8	32.4	25.2	31.8	24.6	9.0	8.3	6.0	23.4
5. % of sequences of each type out of total number of sequences																
of type A	43.7	70.0	66.2	-	52.1	100	75.0	54.0	32.9	47.2	39.0	63.2	50.0	66.7	100	64.3
of type B	48.5	21.1	29.2	-	42.1	0	25.0	46.0	56.1	40.6	47.4	34.2	50.0	33.3	0	35.7
of type V	7.8	8.9	4.6	-	5.8	0	0	0	11.0	12.2	13.6	2.6	0	0	0	0
6. Average number of signals in sequences																
of type A	6.9	8.6	6.6	-	7.6	4.8	13.4	4.0	5.4	10.4	6.4	4.6	5.8	3.5	2.5	15.1
of type B	29.7	17.3	13.6	-	18.0	0	13.7	14.6	14.1	18.0	19.5	17.0	5.9	6.4	0	23.1
of type V	56.8	179.4	70.0	-	104.1	0	0	0	143.2	174.3	110.8	37.0	0	0	0	0
7. Average duration of sequences (s)																
of type A	26.2	35.9	28.0	-	29.4	14.3	32.5	15.6	21.7	44.0	20.0	19.7	25.4	10.0	5.5	51.5
of type B	68.6	43.3	32.1	-	38.7	0	36.5	30.6	37.8	38.7	41.7	34.9	11.9	10.3	0	55.3
of type V	168.8	445.9	242.5	-	286.4	0	0	0	337.3	419.3	237.2	116.0	0	0	0	0
Time of recording (hrs)	6.3	5.7	2.2	2.6	10.0	1.8	1.3	2.4	2.8	10.1	6.9	5.1	2.8	1.0	1.0	3.1

tide there is a drastic decrease of the frequency of occurrence of the type "B" SS, including the communicative and emotional signals; a marked decrease occurs in the number of signals in these and in the average duration of the sequences (Table 23, sections 4, 6, 7). All of this is associated, in the first instance, with the absence of a fish run during the low ebb tide (low tide). To all appearances the large number of social interactions in the feeding locations of the seals is associated with the searching and hunting activity and the cessation of the latter during the low ebb tide led to the observed results.

A strong anthropogenic effect (situation No. 1— people on shore; situation No. 2 — passage of a vessel) leads to a decrease in the number of social interactions of the seals and consequently to a pronounced depression of the signalization by a factor of 5–70 (Table 23, section 2), which also affects the classes of communicative and emotional signals (No. 3 – No. 6, No. 8 – No. 13) to a considerably greater degree. In this case a decrease occurs in the frequency of occurrence of all types of sequences, in the average number of signals within them and in the average duration of the sequences (Table 23, sections 2, 4, 6, 7).

Situation No. 3 — 10–15 minutes after the passage of a vessel — on the basis of many parameters occupies an intermediate position between the No. 1 and No. 2 situations and the "High tide – norm" situation (Table 23). These data provide evidence of the high degree of adaptation of the seals to the effect of the anthropogenic factor, since as early as 5–10 minutes after the passage of the vessel the level of the acoustic activity of the spotted seals attains very high values.

A decrease in the level of signalization with the frequent passage of boats has been noted also for the harp seal (J. M. Terhune et al., 1979).

Table 24

Ethological and acoustical correlates of the Kamchatka spotted seal

Behaviour	Duration of situations	Sound signals associated with behaviour (No. of class)	Number of signals in situation	Number of direct observations
1	2	3	4	5
1. "Patrolling". Slow movement of seal under water along a particular section of the area of water. Waiting for the fish and guarding the section.	1–5 min	No. 2	0–2	72
2. "Ambush". Animal taking up position in "ambush" near wall of pier, at a depth of 2–2.5 m, practically in one place.	up to 2 min	No. 2	0–2	23
3. "Skirmish". Skirmish of two seals under water, blows with fore flippers, possible bites (Figure 15A). Two types of encounter are distinguished:				
a) feature of conflict over fish	2–5 s	No. 11	1–3	18
b) guarding of patrolling section, etc.	1–3 s	No. 6	2–4	4
4. Flight of one of the partners after an encounter, the second partner either immediately or slowly moves after the first (Figure 15B)	2–5 s	No. 2 No. 7	0–2 1–2	3
5. "Pursuit". Pursuit of one animal by another under water at high speed; sometimes may also be continued on the surface. Distance between seals 0.5 –2 m (Figure 16A)	3–5 s	No. 4	1–4	7
6. "Distant threat". Two animals under water remaining immobile, or moving slowly, facing one another at a distance of 3–5 m (Figure 16B)	2–5 s	No. 5	1–2	5
7. "Demonstration" behaviour. Two animals on the surface of the water, at a distance of 1.5–2 m. One seal bends its body in a semicircle with respect to the other, lifts up its head somewhat backwards and periodically immerses in the water first the right and then the left part of the head (Figure 17 B, V). When the partner dives, the second "demonstrating" partner sometimes dives in a spiral with the release of air bubbles.	10–25 s	No. 9 No. 12	1–4 1–6	32

e. Ethological and acoustical correlations

Direct observations from the tower and from the shore, conducted simultaneously with audio-monitoring of the area of water, allowed us for the first time to obtain some

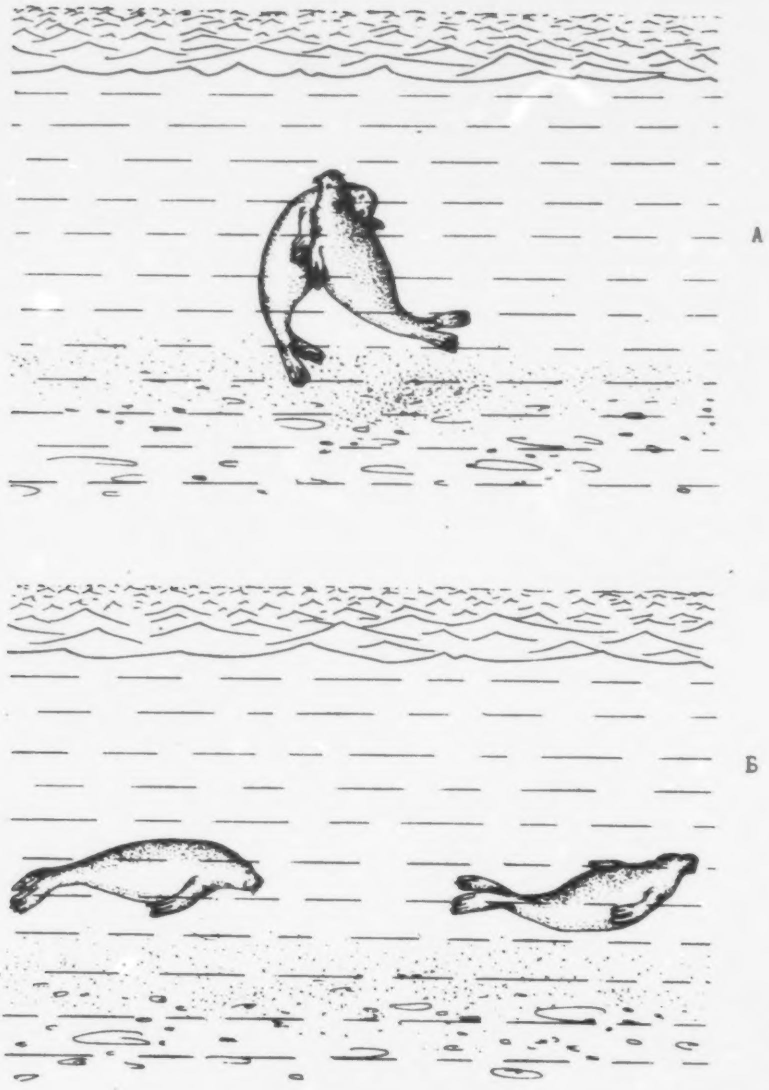

Рис.I5. Социальные взаимодействия камчатской ларги: А - "схватка", Б - "бегство"

Figure 15. Social interactions of the Kamchatka spotted seal: A - "skirmish", B - "flight"

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data on the underwater behaviour of the seals, which was associated with acoustic signals (Table 24). The comparatively small size of the selection of correlations of behaviour and acoustic signalization (164 observations) does not allow us to speak of a strictly monofunctional nature of the communicative and emotional signals (CES), although we

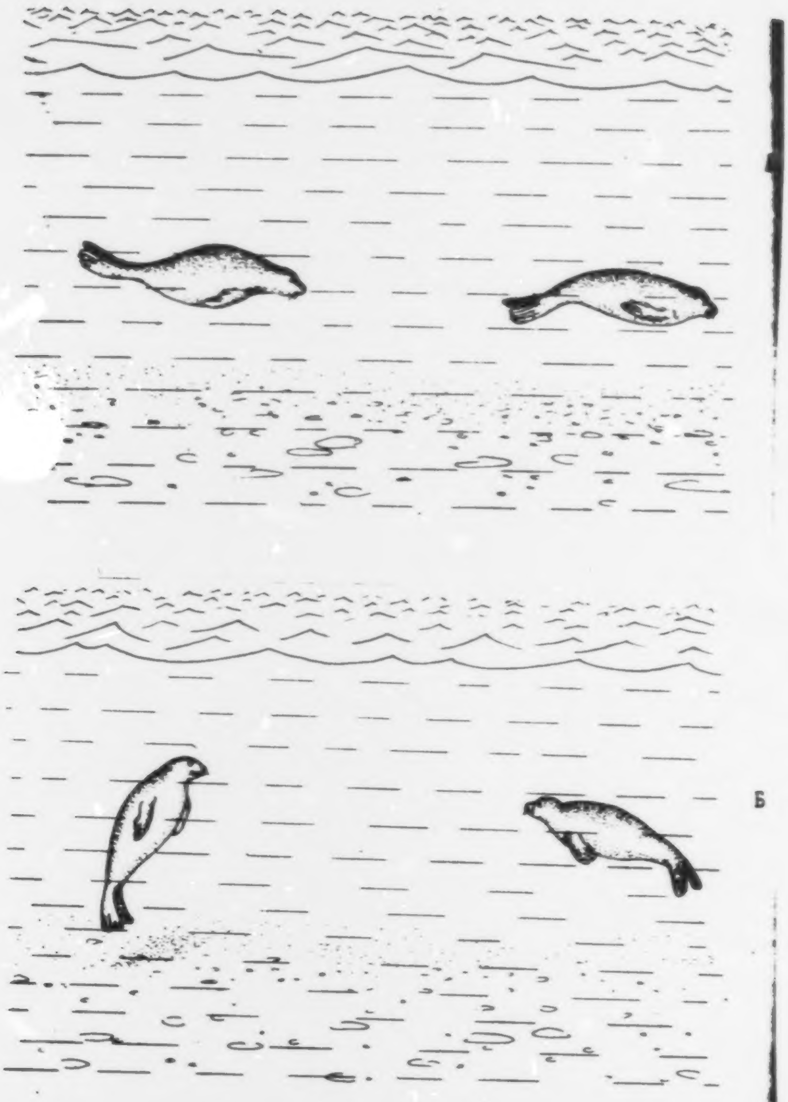

Рис.16. Социальные взаимодействия камчатской ларги: А - "преследование"
Б - "дистантная угроза"

Figure 16. Social interactions of the Kamchatka spotted seal:
A - "pursuit", Б - "distant threat"

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were unable to obtain any data indicating the opposite. At the same time, in the course of the direct observations with the simultaneous monitoring of the area of water we were able to see that a particular sequence of elements of the behaviour, out of those shown in the table, corresponded to the sequences of acoustic signals which included 2–3 of the

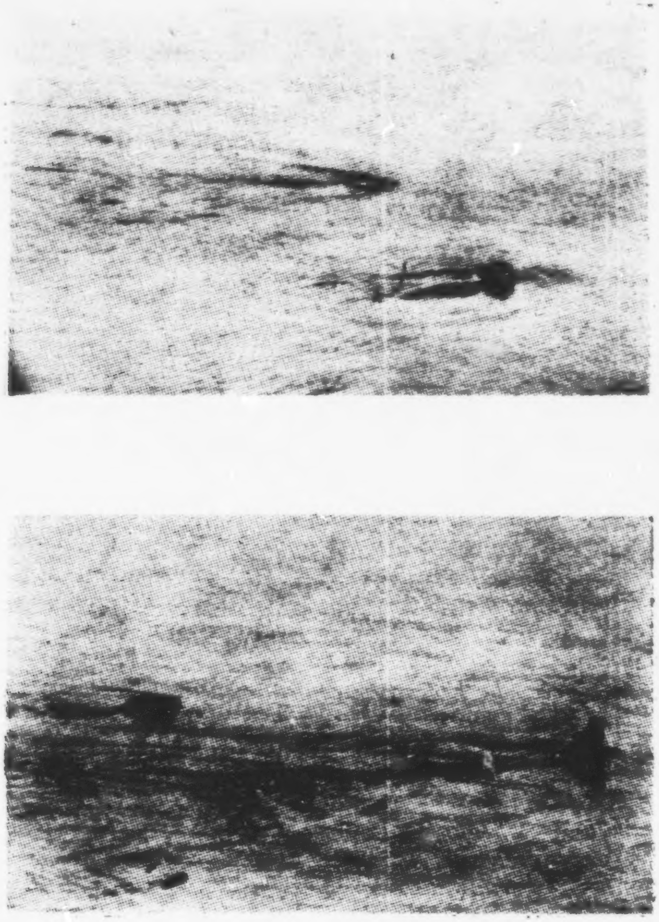

Рис.I7."Демонстрационное" поведение камчатской ларги на поверхности воды (р. Озерная, октябрь I986 г.).

Figure 17. "Demonstration" behaviour of the Kamchatka spotted seal on the surface of the water (Ozernaya river, October 1986).

CES classes. Of interest in our opinion therefore are the data on the frequency of repetition of the signals in the type "A" and "B" sequences, that differ in the composition, duration and number of signals within them (Table 25).

From Table 25 it follows that the maximal repetition frequency of the signals (34.0 signals per minute) is found in sequences that are made up of communicative and emotional signals (CES) of classes No. 3 – No. 6, No. 8 and No. 10 in arbitrary combinations.

Table 25

Characteristics of sequences of acoustic signals of the Kamchatka spotted seal *

Composition of sequences	Number of SS of a given type	Number of signals in SS	Duration of SS (s)	Repetition frequency (sign / min)
Type "A"				
No. 1	47	2–9, av. 3.1	2–46, av. 8.9	21.0
No. 2	234	2–47, av. 5.3	2–235, av. 24.5	15.6
No. 1 + No. 2	139	2–70, av. 10.1	2–383, av. 42.6	15.0
Type "B"				
No. 3 + No. 1, No. 2	15	2–18, av. 7.0	6–71, av. 21.7	19.2
No. 3 + others	62	2–75, av. 20.4	2–194, av. 43.7	28.9
No. 4 + No. 1, No. 2	15	3–19, av. 6.7	4–40, av. 14.9	27.6
No. 4 + others	128	2–75, av. 19.1	2–207, av. 49.8	26.0
No. 5 + No. 1, No. 2	83	2–102, av. 14.0	2–165, av. 43.3	17.1
No. 5 + others	135	3–100, av. 22.9	3–278, av. 56.8	22.9
No. 6 + No. 1, No. 2	27	2–49, av. 10.9	2–92, av. 21.3	30.6
No. 6 + others	116	3–100, av. 22.1	5–207, av. 51.0	25.1
No. 7 + No. 1, No. 2	82	2–80, av. 13.1	3–413, av. 56.9	14.4
No. 7 + others	39	3–59, av. 20.7	8–362, av. 60.5	21.6
No. 3 - No. 6, No. 8, No. 10	49	2–36, av. 5.1	2–91, av 10.8	34.0

* "No. 1" - sequences composed only of signals of class No. 1; "No. 3 + No. 1, No. 2" - sequences having in their composition signals of class No. 3 in arbitrary combinations with signals of classes No. 1 and No. 2; "No. 3 + others" - sequences having in their composition signals of class No. 3 in arbitrary combinations with signals of any other classes, including also classes No. 1 and No. 2. The other abbreviations are interpreted in a similar fashion.

In contrast, the minimal frequency of repetition of the signals (14.4–15.6 signals / min.) was noted in the sequences containing echolocation signals of classes No. 1 and No. 2.

Of the type "A" sequences the largest percentage is made up of SS of class No. 2—double pulses (55.7%), while the smallest percentage (11.2%) comprises SS of class No. 1—single pulses; mixed SS, composed of signals of classes No. 1 and No. 2, occupy an intermediate position (33.1%). If one speaks of the total number of sequences of type "A" and type "B", then the single and double pulses (classes No. 1 and No. 2) are absent in only 6.4% of the sequences. The signals of these classes are produced in 39.3% of the cases in the form of mixed SS together with the CES classes (No. 3 – No. 6, No. 8 – No. 13) and in 54.3% of the cases in the form of sequences composed only of these signals. This indicates the presence in the class No. 1 and No. 2 signals of an important independent function, apparently associated with echolocation (D. Renouf and M. B. Davis, 1982).

Of the sequences which include in their composition CES of any one of the No. 3 - No. 6 classes in arbitrary combinations with the signals of the No. 1 and No. 2 classes the highest percentage is made up of those SS which contain signals of class No. 5 (59.3%) and there are approximately the same percentages of sequences with signals of classes No. 3 and No. 4 (21.4%) and class No. 6 (19.3%)., i.e. in brief interactions of the spotted seal (1–4 signals of any one class of CES No. 3 – No. 6) an encounter is more frequently limited to the threatening sounds of the "distant threat" (signals of class No. 5), and in only 19.3% of the cases was a "skirmish" observed (signals of class No. 6) (Table 25).

The number of sequences that are made up only of the echolocation signals of classes No. 1 and No. 2 and also of any one of the No. 3 - No. 6 classes of CES is lower, by a factor of 1.6–8.5, than the number of mixed sequences which include in their composition communicative and emotional signals of several of the No. 3 – No. 6 classes and signals of classes No.1 and No. 2 (Table 25). In other words, in the mixed SS of the spotted seal, made up of the echolocation signals and the communicative and emotional signals (CES), the signals of each of the No. 3 - No. 6 (CES) classes are produced, on average, 3.1 times more frequently with other classes of CES and markedly more rarely only with the echolocation signals of classes No. 1 and No. 2, i.e. the underwater interactions of the seals usually comprise sequences of behavioural elements.

* * *

Thus, the predominant type of behaviour of the spotted seal in this study region is the searching and hunting activity, in the organization of which acoustic signalization plays an important role. The searching and hunting behaviour of the spotted seal is characterized by waiting tactics; the seal selects the moment for pursuing the fish, or slowly "patrols" its section, or "lies in ambush" (Figure 9). By and large the sections of the area of water are not of equal value from the point of view of their suitability for hunting (Table 21). The large animals of high rank occupy the sections that are most suitable for hunting and they do not admit other seals into these sections. The aggressive encounters, arising during the protection of a section, during a clarification of the hierarchical status of the seals or during a fight over a fish, are accompanied by sequences of communicative and emotional signals (SS), to each of which corresponds a particular sequence of behavioural elements (Table 24). Our observations have revealed for the first time the presence in the spotted seal of group spurts in pursuit of a fish, which markedly increase the probability of the prey being caught. The behaviour of the animals in this case is based entirely on competitive relationships.

Two basic factors affect the frequency of the social contacts of the spotted seal and, correspondingly, the level of the underwater sound activity. These are the intensity of the fish run during the tidal cycle and the disturbance caused by man. As a consequence of this, the highest level of acoustical signalization is noted at high tide, during the night, while the lowest level is noted at the low ebb tide and in situations with a pronounced anthropogenic influence (Table 23). In this case there occurs a decrease in the frequency of occurrence of all types of SS, of the average number of signals within the sequences and of the average duration of the SS (Table 23, sections 2, 4, 6, 7).

As we have already mentioned, the frequency-temporal characteristics that we obtained for the single and double pulses of the spotted seal were found to be similar to the echolocation signals of the common seal. It is quite obvious, however, that it is extremely difficult to obtain direct evidence in the natural habitat for the presence of echolocation signals in the spotted seal. A large number of our observations have shown that the Kamchatka spotted seal during the daylight hours does not make use of the single and double pulses for the echolocation of a fish that is being pursued during a spurt. Similar data were obtained by us in a study of the behaviour and acoustics of the Amur spotted seal.

Evidently, at the stage of pursuing their prey the seals can make do with only sonar detection and the utilization of their vibrissae as a vibro-tactile sensor, perceiving the movement of the water (D. Renouf, 1979, 1980; N. N. Slatina, 1982).

At the same time, by means of the single and double pulses the animals could obtain a kind of static "image", information on the spatial distribution within the area of water of their social partners and other animals, as well as of fish at a particular stage of the search – the "patrolling" and "ambush" (Table 24); by means of series of such signals – information on the movements of neighbouring animals. Also providing evidence for this hypothesis are such data as: the considerable numerical predominance in all situations of the single and double pulses (classes No. 1 and No. 2) as compared with the other classes of signals, which applies especially to situations with a pronounced anthropogenic effect (Tables 3, 5, 7, 8, 13, 16); their wider utilization (by 30–50%) during the night hours (Table 23, section 2); the predominant utilization of these classes of signals during the passage of a boat (situation 2), in the case of the prolonged effect of a disturbance factor; the marked increase (in 60–70% of the cases) in the number of single and double pulses during the eating of a fish by one of the seals (over a period of 1–3 minutes), which, to judge by their intensity, are produced in different sections of the area of water (Figure 18); the considerably smaller drop in the frequency of occurrence of the echolocation signals (classes No. 1 and No. 2) during the low tide and in situations with a high level of anthropogenic effect, as compared with the communicative and emotional signals (remaining classes) (Table 23, section 2).

The acoustic signals of the spotted seal are produced in the form of sequences, and moreover those of them that are made up only of the echolocation signals (classes No. 1 and No. 2) may be emitted by the seals for purposes of orientation and navigation, for detecting other animals and fish at a particular stage of the search. A considerable percentage of all of the sequences comprises mixed sequences (SS of the "B" type), in which are contained both echolocation signals (classes No. 1 and No. 2) and communicative and emotional signals (remaining classes). It may be assumed that in this case the

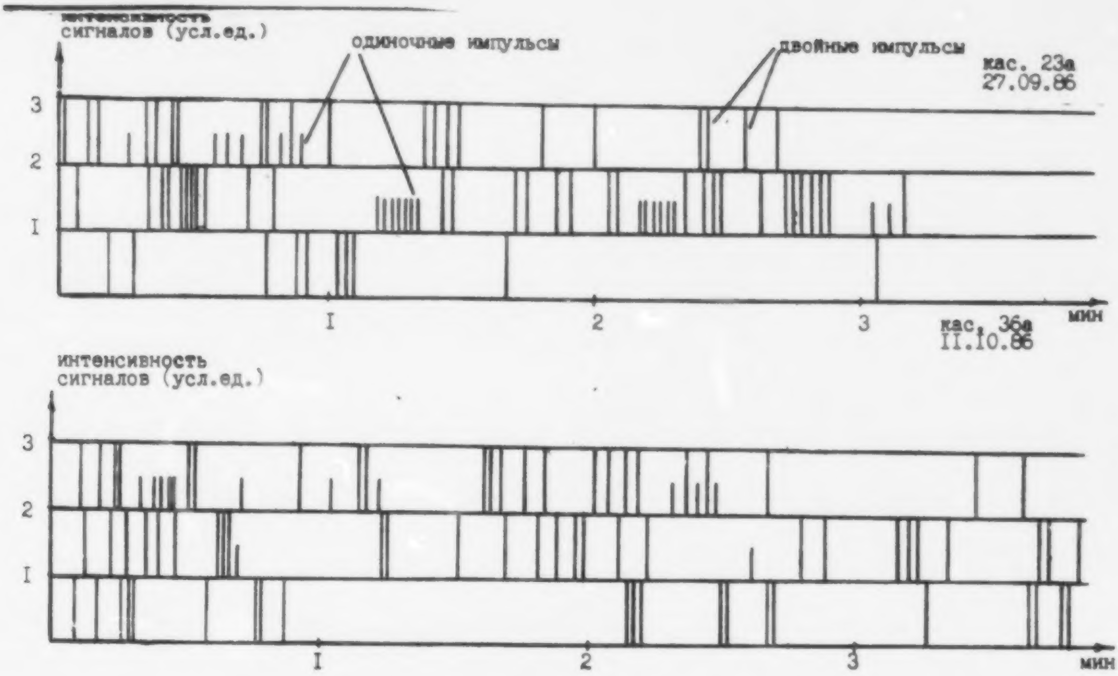

Рис.I8.Использование ларгами одиночных и двойных импульсов в ситуации "зверь с рыбой", объяснение в тексте

Figure 18. The use of single and double pulses by spotted seals in the "animal with fish" situation; explanation in the text.

интенсивность сигналов (усл. ед.) - intensity of signals (conventional units),
одиночные импульсы - single pulses
двойные импульсы - double pulses
кас. 23а, кас. 36а - re. 23a, re. 36a
мин - minutes

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echolocation signals are used for determining the position of the body of the partner or partners, and with the approach and direct interaction of animals various classes of communicative and emotional signals are emitted. The duration and degree of expression of such contacts are affected by both external factors, for example, disturbance by man, as well as internal factors, such as the age of the partners, their social status, etc.

Chapter 3. Underwater sound signalization of the bearded seal (*Erignathus barbatus* Erxleben, 1777) and the ringed seal (*Phoca hispida* Schreber, 1775)

1. The bearded seal (*Erignathus barbatus* Erx., 1777)

The initial interests of the expedition in the study of the under-ice acoustical signalization of the seals of the White Sea were associated with the ringed seal (as the only species living on the persistent fast ice according to the data of the PINRO [Polyarnyi nauchno-issledovatel'skii institut morskogo rybnogo khozyaistva i okeanografii imeni N. M. Knipovicha — The M. N. Knipovich Polar Scientific Research Institute of Marine Fisheries and Oceanography]). However, our investigations in the zone of the persistent fast ice in Konyukhovaya Bay (Summer shore of the White Sea) noted a high level of sound activity of the males of the bearded seal, characteristic of this species during the reproductive period (C. Ray et al., 1969).

a. Acoustic signals

A spectral-temporal and auditory analysis of about 3 thousand signals has allowed us to distinguish and describe 5 principal classes of acoustic signals of the bearded seal. Some of the frequency-temporal characteristics of the principal classes of signals of the bearded seal are presented in Table 26. All of the principal classes of signals of the bearded seal comprise protracted, whistle-like, frequency modulated signals.

Table 26

Some frequency-temporal characteristics of the signals of bearded seal males (March–April 1984)

Class of signals	Duration of signals (s)	Dominant frequency (kHz)		Number of spectrally analyzed signals; percentage of signals of the given class out of the total number of signals (2918); name of class, comments
		initial	ultimate	
1	2	3	4	5
No. 1	0.7–3.0	2.0–3.0 av. 2.5	0.3–0.7	11; 44.9%; "Whistle" (Figure 19A, B;). The initial frequency of the "long whistles" (7 signals, with a duration of 1.3–3.0 s, av. 1.8 s) is 2.0–3.0 kHz, av. 2.5 kHz, ultimate – 0.3 kHz. During the first 0.5 s there occurs a drop in the dominant frequency to 1.4–2.1 kHz, av. 1.7 kHz. The initial frequency of the "short whistles" (4 signals, with a duration of 0.7–0.9 s, av. 0.78 s) comprises 0.8–1.5 kHz, av. 1.3 kHz, ultimate – 0.3–0.7 kHz, av. 0.5 kHz. Signals of this class are produced in series (2–5) after a short pause of 1-2 s following signals of the "long trill" and "short trill" classes. Duration of pauses between "long whistles" – 4-5 s, between "short whistles" – 0.9–1.0 s.
No. 2	2.9–11.6	0.6–5.6 av. 2.7	0.3–1.6 av. 0.5	10; 23.0%; "Short trill" (Figure 19V). During the first 0.5 s the drop in the dominant frequency comprises 0.1–2.1 kHz, av. 0.9 kHz.
No. 3	34.2–61.4	3.0–6.2 av. 4.1	0.3	10; 18.3%; "Long trill" (Figure 20). During the first 0.5 s the drop in the dominant frequency occurs especially rapidly and comprises 0.3–2.7 kHz, av. 1.2 kHz. Approximately 5-7 s after the beginning of the signal transitory pulsations of the fundamental frequency are noted (12–18), with a duration of 0.12–0.15 s, with an increase of the frequency by 0.2–0.5 kHz. As the signal is produced, after 20–32 s, there are observed 2–4 rises of the dominant frequency by 0.4–0.5 kHz, with a duration of 3–9 s, with a following smooth fall to the value of the ultimate frequency.
No. 4	48.0–78.2	4.6–6.8 av. 6.1	0.3–0.5 av. 0.36	6; 9.2%; "Intermittent trill" (Figure 21A;). During the first 0.5 s the drop in the dominant frequency occurs especially rapidly and comprises 0.4–1.6 kHz, av. 1.1 kHz. Rather than in a continuous fashion, each signal is produced in segments (9–15 segments in a signal), that are separated by pauses with a duration of 0.2–1.7 s. Duration of first segment 4–11 s; during it are encountered transitory pulsations, which become longer towards the end of the segment, of the dominant frequency (12–18), with a duration of 0.3–0.75 s, with an increase by 0.4–0.6 kHz and a subsequent decrease in the frequency. The drop in the dominant frequency as a whole from the beginning of the first segment and up to its end comprises 1.1–4.2 kHz, av. 3.1 kHz. The average duration of the pauses between the first 4-5 segments is less, by a factor of 1.3–2.6, than that between the following segments. Duration of 2nd segment 0.12–0.52 s, duration of each following segment 1.1–2.5 times greater than the preceding segment. Initial frequency of second–fifth segments scarcely changes at all and comprises 2.6–3.4 kHz; the drop in the dominant frequency during each of these segments is 0.2–0.9 kHz. The initial frequency of the following segments decreases from segment to segment by 0.2–0.6 kHz and comprises 1.5–2.8 kHz; the drop in the dominant frequency during each of these segments is 0.6–1.5 kHz.
No. 5	3.5–10.6	0.3–0.7 av. 0.4	0.3–0.4 av. 0.33	12; 4.6%; "Lilting trill" (Figure 21B;) In the signals there may be distinguished ascending and descending sections, in which there occurs, correspondingly, an increase and a decrease in the dominant frequency. The duration of the ascending section comprises 2.2–7.2 s, av. 3.8 s. Maximal frequency of signals 0.8–1.6 kHz, av. 1.4 kHz. The duration of the descending section also varies, from 1.2 to 8.1 s, av. 3.2 s.

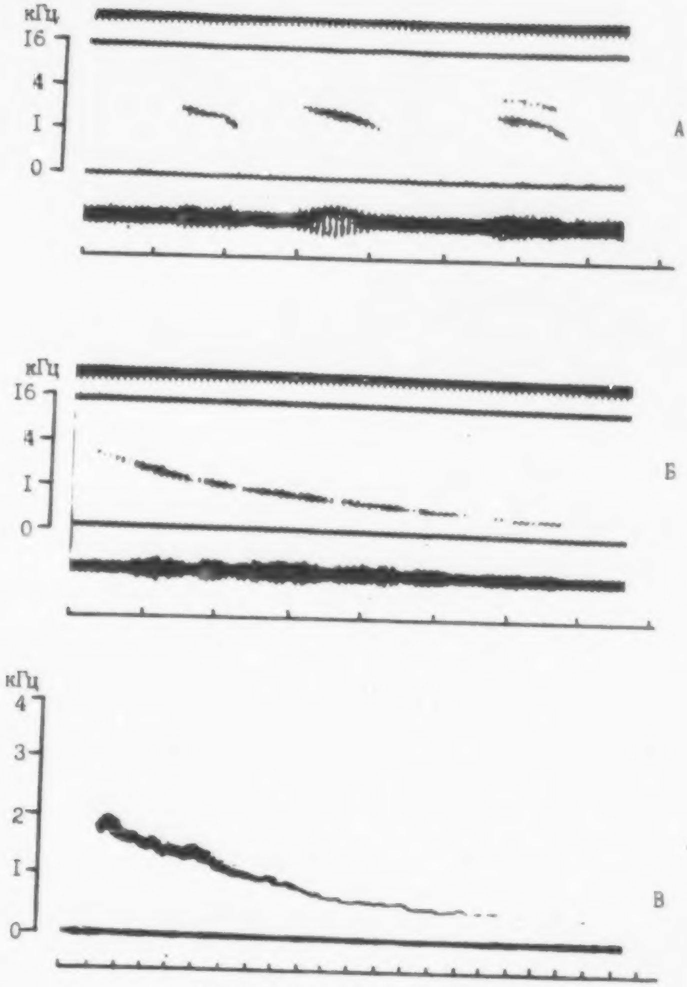

Рис.I9.Акустические сигналы морского зайца основных классов
А,Б - № I; В - № 2.

Figure 19. Acoustic signals of the principal classes of the bearded seal
А, Б (A, B) - No. 1; В (V) - No. 2.
ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

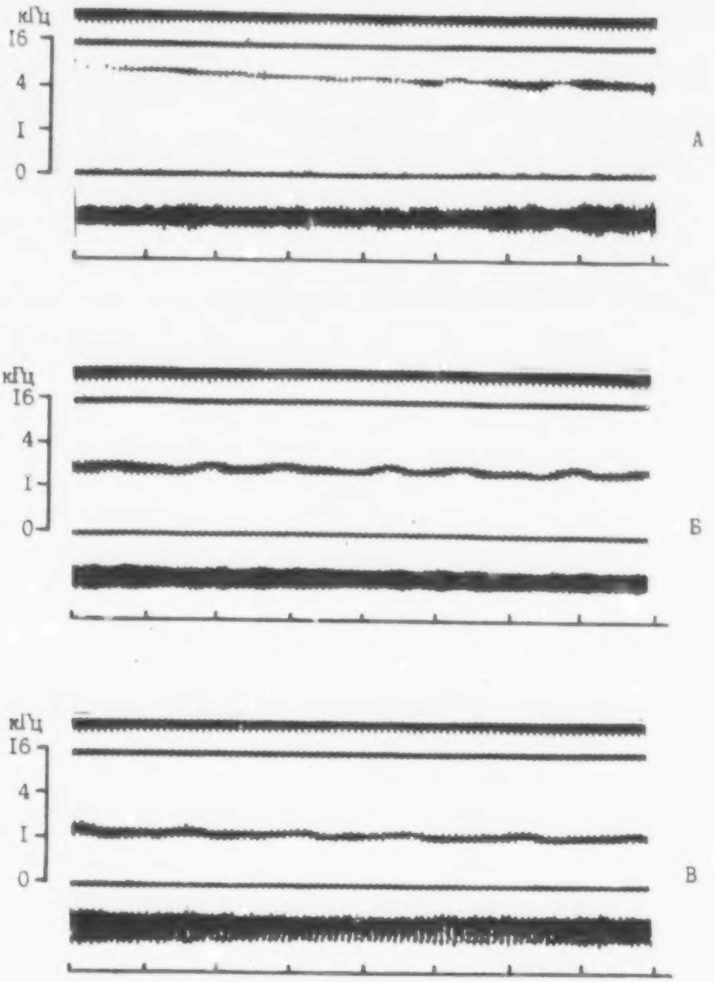

Рис.20.Акустические сигналы морского зайца основных классов:
А - № 3 (фрагмент начальной части сигнала);
Б,В - № 3 (фрагменты средней части сигналов)

Figure 20. Acoustic signals of the principal classes of the bearded seal:
А (A) - No. 3 (fragment of initial part of signal);
Б, В (B, V) - No. 3 (fragments of middle part of signals)
ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

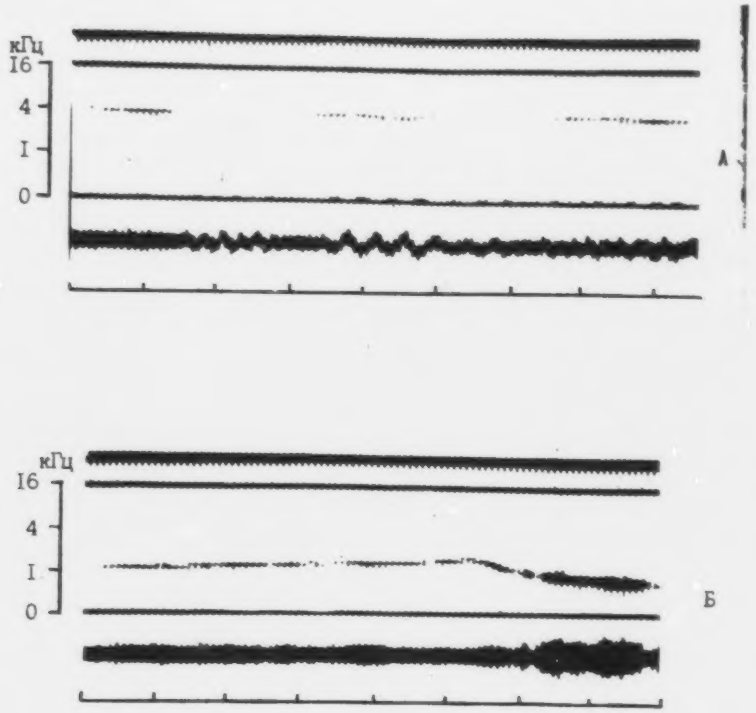

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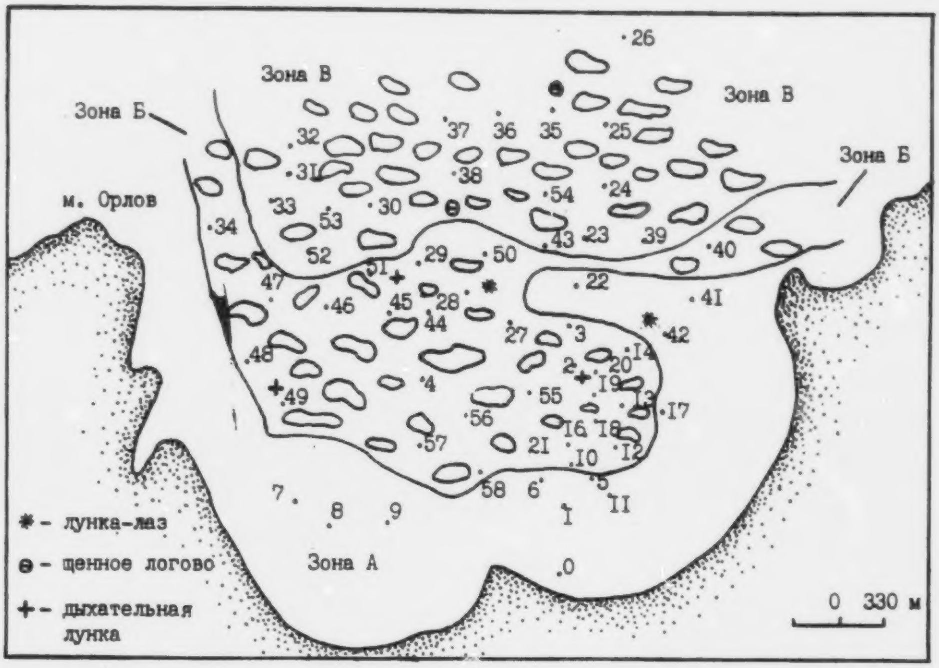
Рис.2I.Акустические сигналы морского зайца основных классов:
А – № 4(фрагмент начальной части сигнала);
Б – № 5 (фрагмент начальной части сигнала).

Figure 21. Acoustic signals of the principal classes of the bearded seal:
А (A) - No. 4 (fragment of initial part of signal);
Б (B) - No. 5 (fragment of initial part of signal)
ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

b. Features of the distribution and of the sound signalization under ice during the spring

The study of the sound activity of the bearded seal in the region of the fast ice in Konyukhovaya Bay in the White Sea in March-April 1984 was carried out in three zones: zone A — even ice field, zone B — sparse low hummocks and zone V — fields of hummocks, up to 1.5 m in height. The locations of the measurement points in these zones are shown in Figure 22.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Зона В
Зона Б
Зона В
Зона Б
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I6
I8
57
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I0
I2
58
6
5
II
7
8
9
I
Зона А
0
✱ - лунка-лаз
ɵ - щенное логово
+ - дыхательная лунка
0 330 м

Рис.22.Схема района подледных исследований (Конюхова губа, Белое море,март-апрель 1984 г.)

Figure 22. Schematic map of the region of the studies under the ice (Konyukhovaya Bay, White Sea, March - April 1984).

зона А - zone A, зона Б - zone B, зона В - zone V
м. Орлов - Cape Orlov
✱ - лунка-лаз - hole in ice for emergence
θ - щенное логово - pupping den
+ - дыхательная лунка - breathing hole

In Tables 27, 28 and 29 are presented the average index of signals per minute, the average intensity of a large part of the signals and the maximal noted numbers of males of the bearded seal at each measurement point correspondingly in zones A, B and V.

From Table 27 it follows that for zone A (even field) the average value of the signals per minute is equal to 1.1 ± 0.29, while the intensity of the signals on average throughout the zone comprised 0.9 ± 0.18. This indicates that in this zone only a few individual animals are encountered.

Table 27.

Characteristics of the acoustical activity and numbers of males of the bearded seal in zone A (March–April, 1984)

No. of measurement point	0	1	5	6	7	8	9	11	17	22	41	42
Average index of signals / minute	0.7	1.4	0.7	0.9	0.8	0.8	0.5	1.5	1.7	4.1	0.3	0.2
Average intensity of signals	0.5	1.1	1.5	1.0	0.5	0.5	0.5	1.0	1.0	2.5	0.5	0
Maximal numbers	0	2	0	0	0	0	0	2	1	4	0	0
Number of measurements (15 minutes)	1	11	1	1	1	1	1	5	1	1	1	1

In zone B (sparse hummocks) the average value of the index of signals per minute is higher and is equal to 2.5 ± 0.17 (Table 28). The intensity of the signals on average throughout the zone comprised 1.7 ± 0.07. The average maximal number of males of the bearded seal within the radius of the effective operation of the hydrophone in zone B was equal to 2.5 ± 0.14.

In zone V (fields of hummocks) the average value of the signals per minute index is equal to 4.2 ± 0.21, while the average intensity of the signals throughout the zone comprised 3.1 ± 0.09 (Table 29). The average maximal number of males of the bearded seal within the radius of the effective operation of the hydrophone in zone V was equal to 4.4 ± 0.16.

Thus, the largest number of seals is found in zone V (fields of hummocks, up to 1.5 m in height).

Daily activity. As a result of the measurements there was found an increase in the level of the sound activity of the bearded seal during the evening hours. Data on the level of the acoustical activity of bearded seal males in zone V (hummock fields) at different times of day are presented in Figure 23. The average value of the signals/minute index between 07.00 and 15.00 hours comprised 3.1 ± 0.20, while between 15.00 and 19.00 hours it was 4.7 ± 0.16. The analysis showed a significance of the differences of the data

Table 28.

Characteristics of the acoustical activity and numbers of males of the bearded seal in zone B (March–April, 1984)

No. of measurement point	Average index of signals / minute	Average intensity of signals	Maximal number	Number of measurements (15 minutes)
2	3.0	2.2	4	15
3	3.7	1.8	4	3
4	2.4	1.6	3	2
10	2.7	1.5	3	5
12	1.8	1.5	2	7
13	1.7	2.0	2	9
14	2.4	1.5	2	2
15	2.9	1.6	3	4
16	2.0	1.5	2	1
18	3.5	2.8	2	4
19	3.1	2.3	2	3
20	2.8	2.3	3	6
21	1.9	1.3	3	1
27	1.0	1.5	1	1
28	1.6	2.0	3	1
29	3.1	2.0	3	1
34	1.6	1.5	3	1
40	1.5	2.0	1	1
44	3.0	1.5	3	1
45	2.5	1.5	3	1
46	1.6	1.3	2	1
47	2.1	1.3	2	1
48	1.3	1.3	2	1
49	1.4	1.3	2	1
50	3.1	1.3	3	1
55	5.1	1.5	3	1
56	3.7	1.5	3	1
57	3.2	1.0	2	1
58	3.9	1.3	2	1

in these time intervals. The increase in the level of signalization (by a factor of 1.3–3.5 times) in the second half of the day, commencing at 15.00 hours, is also indicated by the measurements that were carried out over the course of a single day in particular points of zone V (point 26, 13.00–15.00 hrs – 3.8 signals/minute; 15.00–18.00 hrs – 4.9 signals/ minute; point 43, 14.00–15.00 hrs – 1.5 signals/minute; 18.00–19.00 hrs – 5.2 signals/ minute).

On the whole, however, the acoustical signalization of the bearded seal is characterized by having a comparatively constant level (Figure 23). The coefficient of

Table 29.

Characteristics of the acoustical activity and numbers of males of the bearded seal in zone V (March–April, 1984)

No. of measurement point	Average index of signals / minute	Average intensity of signals	Maximal number	Number of measurements (15 minutes)
23	3.2	3.1	4	13
24	4.0	3.5	5	1
25	3.7	3.1	5	2
26	4.5	3.5	5	17
30	3.5	3.0	4	1
31	5.1	3.3	4	1
32	6.0	3.5	5	1
33	4.9	2.8	4	1
35	3.7	3.3	5	4
36	4.9	3.5	5	2
37	4.9	3.5	5	2
38	5.3	3.3	5	1
39	2.4	2.5	3	1
43	3.6	3.3	5	9
51	4.4	2.3	4	1
52	4.1	2.5	4	1
53	4.1	3.0	4	1
54	3.1	3.5	4	1

variation of the signals/minute indices has a small value — 4.2% (data for zone V). A fairly constant level of signalization is found also in some individual points (Figure 24, measurement over the course of 15 minutes at point 43).

The formation of the fast ice in Konyukhovaya Bay in 1987 proceeded in a different fashion from that in 1984, as a result of which the transitional zone B (sparse hummocks) was practically absent, and the even ice fields (zone A) passed directly into the fields of hummocks (zone V, Figure 25). The data on the intensity of the signals and the numbers of males of the bearded seal in the A and V zones are presented in Table 30. As we can see, on the whole they corroborate the principal conclusion of the 1984 season: the largest numbers of seals are found in zone V (fields of hummocks, up to a height of 1.5 m).

The study of the acoustical activity in the immediate vicinity of the edge of the fast ice and in the open water allowed us to establish that the barrier of the hummocks, forming the edge of the fast ice, is a serious obstacle for the signals of the seals. Thus,

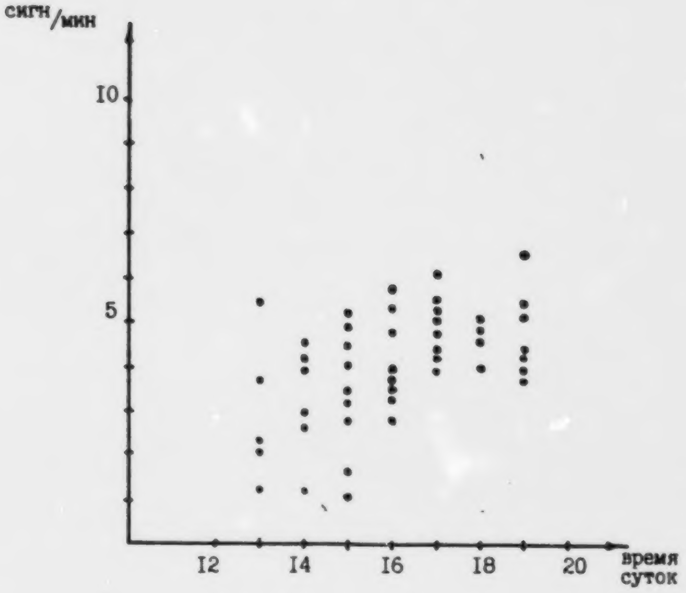

Рис.23.Динамика уровня акустической активности морского зайца в различное время суток(данные по зоне В,март-апрель 1984 г.)

Figure 23. Dynamics of the level of acoustical activity of the bearded seal at different times of day (data for zone V, March–April, 1984).

ordinate сигн / мин - signals / minute

abscissa время суток - time of day

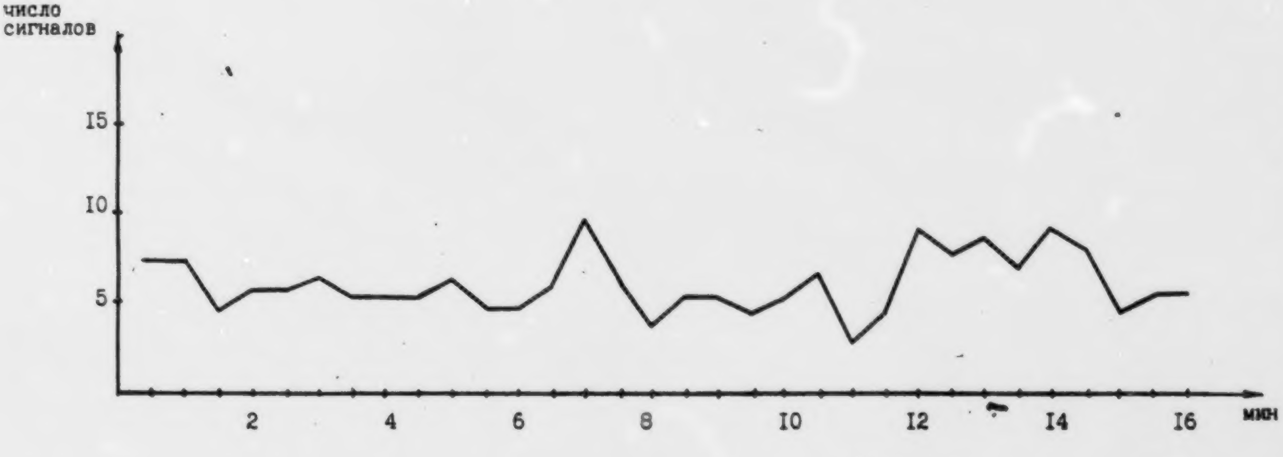

Рис.24.Динамика уровня звуковой сигнализации морского зайца (т. 43, зона В).

Figure 24. Dynamics of the level of sound signalization of the bearded seal (point 43, zone V).

ordinate число сигналов - number of signals

abscissa мин - minutes

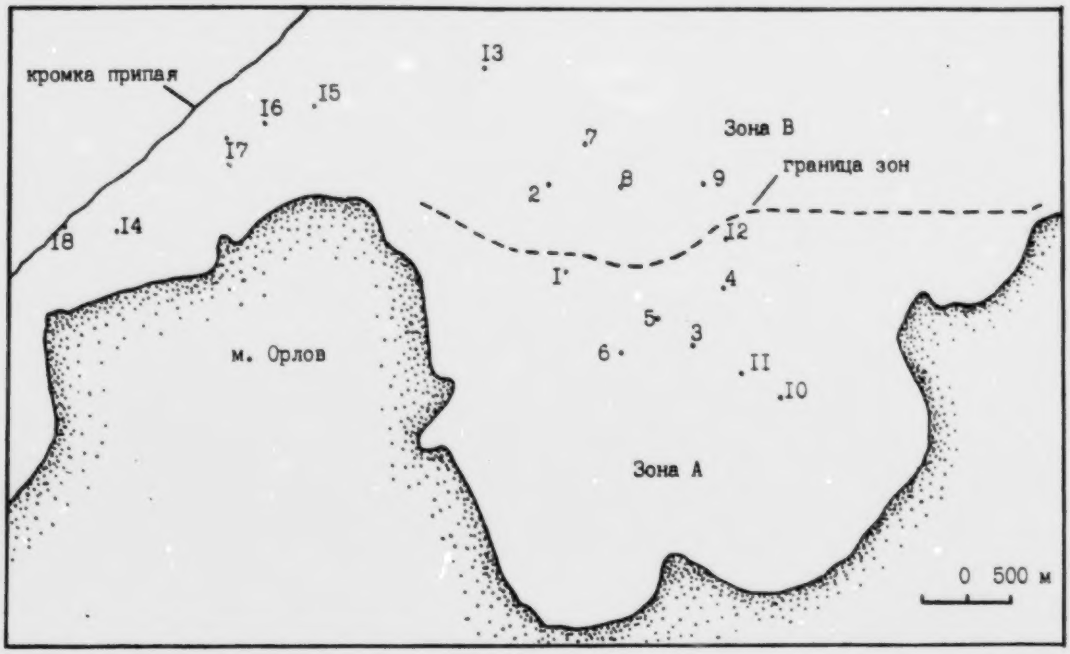

Рис.25.Схема района подледных исследований (Конюхова губа, Белое море, март-апрель I987 г.)

Figure 25. Schematic map of the region of the studies under the ice (Konyukhovaya Bay, White Sea, March–April 1987).

кромка припая - edge of fast ice
зона А - zone A, зона В - zone V
граница зон - boundary between zones
м. Орлов - Cape Orlov

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already at a distance of 70 m from the edge of the ice (point 14) no signals were noted (Figure 25), while on the open water (point 18) the intensity of the sounds was high. The observations showed the presence of animals in the area of water close to the edge of the fast ice. All of this indicates that all of the signals recorded by us were produced by seals that were living at this time in the region of the fast ice between the edge of the fast ice and the shore.

The studies that were carried out in 1987 together with the SevPINRO [Severnyi Polyarnyi nauchno-issledovatel'skii institut morskogo rybnogo khozyaistva i okeanografii - Northern Polar Scientific Research Institute of Marine Fisheries and Oceanography] (V. A. Potelov and others) revealed a marked correspondence of the data on the numbers

Table 30.

Characteristics of the signal intensity and estimation of the numbers of the bearded seal in zones A and V (March–April, 1987)

No. of measurement point	Zone A								Zone V								
	1	3	4	5	6	10	11	12	2	7	8	9	13	15	16	17	18
Average intensity of signals	3.5	2.0	2.0	2.0	2.0	1.5	1.0	2.5	3.5	3.0	3.0	3.0	3.5	3.5	3.5	3.5	3.0
Maximal recorded number	3	2	3	3	2	1	1	3	5	3	3	3	4	4	2	2	2
Number of measurements (15 minutes)	2.7	6.4	2.1	2.1	2.1	4.3	2.1	2.1	11.9	2.1	6.4	4.3	2.1	2.1	2.1	4.1	1.2

Table 31.

Estimation of the numbers of White Sea seals in Konyukhovaya Bay

Parameters	Zone A	Zone V
	Traditional method	
Density of holes (no./ km^2)	6–40	–
Density of dens (no./ km^2)	0	10–12
	Acoustical method	
Numbers of seals of both species in points zonal points	1–3 (points 3 -6,10, 11, Figure 5)	6–8 (points 2, 13, Figure 5)

and distribution of the seals, obtained by means of the traditional methods for estimating population numbers (searching for dens with dogs) and by the acoustical method (Table 31).

The information on the ice period in the life of the bearded seal is incomplete and occasionally it is also contradictory. The pupping period extends from the middle of March to the beginning of May, but in the literature there is no single opinion on the subject as to on what ice, drifting ice or fast ice, the females give birth to and feed their young.

Most authors consider the bearded seal to be a denizen only of drifting ice (K. K. Chapskii, 1976). At the same time there are data which indicate that in the Barents Sea the birth of the young occurs on the drifting ice or in the region of the fast ice along the shore (K. K. Chapskii, 1938). The holes of the seals may be located both close to the shore as well as in the depths of the bay (L. A. Popov, 1939); in the Sea of Okhotsk several openings or holes of the "lakhtak" [the Pacific subspecies of *E. barbatus* Erx.] have been found situated close to one another by investigators on more than one occasion (G. A. Fedoseev, 1971). The bearded seal of the Canadian Arctic also spends much time in the zone of the persistent fast ice (M. C. Kingsley et al., 1985).

Emergences of young bearded seals through the holes onto the thick spring ice in the fast ice zone have been observed in Rusanova Bay, in the Petukhovskii Shar Strait and of the southern shores of Novaya Zemlya (V. A. Potelov, cited by: K. K. Chapskii, 1976).

On the White Sea findings of the bearded seal during the winter are known in the northern part of Onezhskaya Bay, the south-eastern portions of Dvinskaya Bay and the eastern regions of the Kandalakshskiy Gulf (K. K. Chapskii, 1976). The pupping regions are considered to be the drifting ice in the northern part of the White Sea and the south-eastern part of the Barents Sea. This however contradicts the fact that every year at the end of April and in May young of the bearded seal are caught at Lopshen'ga and at Letnyaya Zolotitsa, and in June – in the closed end of Onezhskaya Bay and in the estuary of the Severnaya Dvina, i.e. 500–600 km to the south of their hypothetical place of birth. It is barely credible to suggest that one and a half to two months after their birth the young of this species, considered to be nonmigratory, had accomplished such migrations. In the region of our studies the bearded seal young of the current year, according to the reports of local inhabitants, appear in the mixed rookeries of the ringed and bearded seals immediately after the break up of the ice cover (end of April – beginning of May).

The question as to where (on the ice or in a snow pupping den) the birth of the young bearded seal occurs on the fast ice may be resolved unambiguously. Neither in the course of special studies on the fast ice during the period of the reproductive season (L. P. Lukin and V. A. Potelov, 1978) nor by the local inhabitants was there a single case noted of the finding of a young pup of the bearded seal on the ice. The presence of predators that inspect the fast ice (wolf, fox) may also be included among the factors which limit the opportunity for the birth and feeding of the young pup outside of the snow shelter.

It is considered that the construction of snow lairs and shelters is not characteristic of this species (K. K. Chapskii, 1976). At the same time there is noted in the literature the possibility of pupping by the bearded seal in snow dens on the Kara Sea (L. G. Rutilovskii, 1939) and on the fixed ice of the bays along the coast of Siberia (N. P. Smirnov, 1927). Of interest in connection with this also are the data on the dimensions of the dens of the ringed seal, which have been found on the fast ice of the White Sea: length — 150–300 cm, width — 60–80 cm, greatest height — 40–60 cm (L. R. Lukin and V. A. Potelov, 1978). Besides these, there have also been found dens of considerably larger dimensions (correspondingly: 8 m, 1.5 m and 1 m), which these investigators also assigned to those constructed by the ringed seal. A considerable difficulty in the identification of a den of a bearded seal female lies in that its young, which moulted in the embryonic state, in contrast to the white-coat of the ringed seal, are able to get away from observers into the water. On the basis of the data from the acoustical method and summing up the information presented above, we may assume, with a large measure of probability, the existence of two ecotypes of the bearded seal, reproducing – the one in the open on the drifting ice and the other in snow pupping dens on the persistent fast ice, in a fashion similar to that found in the ringed seal (G. A., Fedoseev, 1975).

c. Acoustic signalization during the summer months

In July–August 1986 studies on the sound activity of the bearded seal were carried out on an area of water near Letnyaya Zolotitsa, situated 30 km from the site of the winter studies in Konyukhovaya Bay. Time of tape recording — 67 hours; of audiomonitoring

— more than 500 hours. We were able to record 121 signals of the bearded seal (75.2% signals of classes No. 2 and No. 3; 20.7%— signals of class 5; 4.1% — No. 1), i.e. there was practically no signalization. All of the signals were of a fragmentary character and were produced during the presence of beluga in this area of water; in some cases during the movement of the beluga in the immediate vicinity of the bearded seal. Visual observations made during a complete calm indicate that the animals probably occupy particular portions of the area of water during the course of the day (600–800 m from the shore, at a distance of 1–2 km from one another), taking up positions on the surface in the characteristic "lying" posture. It is possible that the observed sound reaction of the bearded seal is associated with the intrusion of a beluga into a portion of the area of water, that is occupied by the seal.

Not a single signal of the bearded seal could be recorded during the summer (10–20 August, 1986) in the region of the winter studies (Konyukhovaya Bay) when the area of water was monitored for sound in the immediate vicinity of the mixed hauling-out grounds of the bearded seal and the ringed seal (total time of audio-monitoring — 28 hours). The hauling out grounds were located on a stony island, at a distance of 400 m from the shore, and the maximal number of bearded seals here was 20. Distance between resting seals — 10–20 m.

The use of the acoustical method makes it possible to establish the fact of the presence and reproduction of this species on the persistent fast ice. In the Russian literature as long ago as 1937 there was noted the characteristic peculiarity of the bearded seal for producing whistle-like sounds during the period of reproduction (A. N. Dubrovskii, 1937). In our studies we have also based ourselves on the data obtained by American scientists in a study of the sounds of the "lakhtak" — the Pacific subspecies of the bearded seal (C. Ray et al., 1969). The thoroughness with which these investigations were carried out leaves no doubt that the sounds were indeed produced by sexually mature males of the "lakhtak" in the nuptial state, at the height of the reproductive season. Similar signals were recorded by us in the region of our studies.

The stereotypical nature and recurrence of the signals, the high level of acoustical activity of the White Sea bearded seal during the reproductive period and its relative constancy (Figures 23 and 24) are apparently determined by the function of the sound signals, associated with the reproductive and territorial behaviour. This is also indicated by the practical cessation of vocalization during the summer months, in spite of the presence of animals in the area of water. Thus, our data are in agreement with the hypothesis about the territorial and reproductive functions of the signals of the lakhtak, mentioned previously (C. Ray, 1969). Investigators have included among the functions of territorial protection also the stereotypical recurring trills produced by the mature males of Weddell's seal (C. Ray, 1967). Stereotypical, recurring sequences of acoustical signals, which were produced only during the reproductive season, were found in the mature males of walruses, protecting the area of water around an ice floe with females (C. Ray and W. A. Watkins, 1975).

Deserving attention, in our opinion, is the hypothesis about the echolocation function of the signals of the bearded seal (T. C. Poulter, 1966). It is probable that the animals to some degree utilize their prolonged, frequency-modulated signals for detecting those like themselves under the conditions of the low illumination under the ice.

There are some differences in the signalization of the different subspecies of the bearded seal. The signals of the White Sea seals do not have in their initial part the segment of increasing frequency and the short moan, following the pause after the principal trill, as was noted in the lakhtak (C. Ray et al., 1969). Also differing is the initial frequency of the sounds in the White Sea (3.0–6.8 kHz) and Pacific (2.0–3.0 kHz) subspecies. The signalization in the White Sea, according to our data, was by and large markedly more diverse, although it is quite possible that much of what has been said above may be explained by the small selection of signals obtained by the American investigators (C. Ray et al., 1969). Studies carried out in the Canadian Arctic indicate that a certain number (up to

18%) of the sounds of the bearded seal belongs to signals that have an ascending portion – "lilting trill" (class No. 5) (J. Stirling et al., 1983). In this study there is also cited a higher initial frequency of the trills (up to 6 kHz) than in the paper of C. Ray et al. (1969). Further studies are necessary to elucidate the degree of geographical variability of the signalization of this species.

2. The ringed seal (*Pusa hispida* Schreber, 1775)

The study of the acoustical activity and distribution of the ringed seal under the ice in the region of the persistent fast ice in Konyukhovaya Bay (White Sea) in March–April 1984, as for the bearded seal, was carried out in three zones: zone A— even ice field, zone B — sparse small hummocks, and zone V— fields of hummocks, up to 1.5 m in height (Figure 22).

The study of the fast ice in these zones allowed us to find two dens, three breathing holes and 2 emergence holes of the ringed seal. The dimensions of the pupping dens and their configuration are presented in Figure 26. In both dens there were found "small basins"[11], filled with wet snow. Apparently, as a result of the warming of the chamber by the warmth, radiated by the animal, and also of the evaporation of water from the bottom of the den, the walls were covered with ice to about 1 cm. The presence in both dens of diving holes with a diameter of about 20 cm provides evidence of their use by the young animals, although the latter themselves could not be found.

The upper diameter of the breathing holes comprised 15, 16 and 20 cm. Each of them had the form of a truncated cone, with the lower diameter attaining a size of about 60 cm. The walls of the holes bore numerous traces of the claws of the seals.

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[11] Russian "vannochka", diminutive of "vanna" - bath tub, is the word translated here by "small basin". [Tr.]

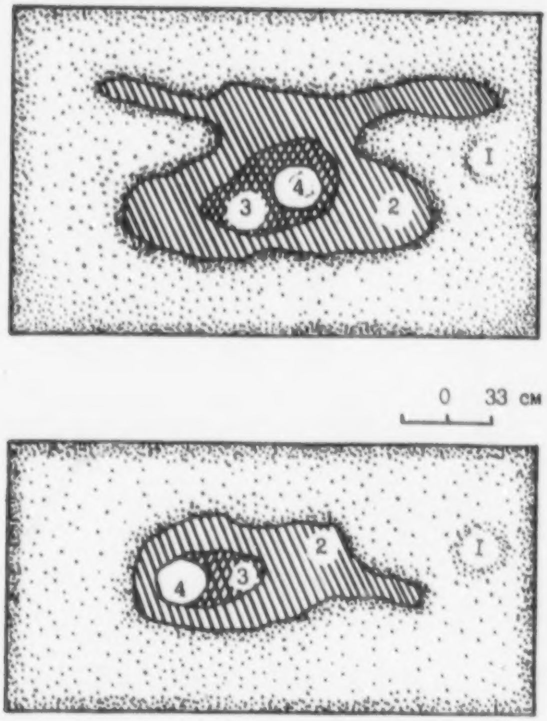


Рис.26.Формы детного логова кольчатой нерпы (I – снежный покров; 2 – основание логова; 3 – "ванночка"; 4 – лунка-лаз).

Figure 26. Forms of a pup's den of the ringed seal
(1 - snow cover; 2 - floor of den; 3 - "small basin"; 4 - emergence hole).

Moreover, on April 5th–6th we were able to find emergence holes of the grey pups of the ringed seal, located on the open ice. The upper diameter of the emergence holes of the grey pups of the ringed seal comprised 37 and 40 cm. Evidently they are enlarged breathing holes. The grey pups are fairly careful and they slip down into the water when a man approaches to closer than 80–90 m. Within a radius of up to 2-3 m from the emergence hole traces of the seal's sojourn were visible: the snow was tamped down and on it were numerous traces of the claws of the seal's fore flippers. In addition to the impressions of the small fore flippers of the grey pup, impressions were also noted of the claws of an adult animal. The formation of the more numerous rookeries of the ringed seal on the spring ice occurs later, commencing from the middle of April (V. A. Potelov, 1978).

a. Sound signals

A spectral-temporal analysis and an auditory analysis of more than 4.5 thousand signals allowed us to distinguish and describe 5 principal classes of sound signals of the ringed seal. Some of the frequency-temporal characteristics of the principal classes of signals of the ringed seal are presented in Table 32.

b. Features of the distribution and of the sound signalization under ice during the spring

Measurements of the level of acoustical activity were carried out in all zones; the location of the measurement points are shown in Figure 22. The data obtained are presented in Tables 33–35. From Table 33 it follows that in zone A (even ice fields) the average value of the signals per minute index is equal to 0.6 ± 0.30, while the intensity of the signals is greater than zero in only a few points. Thus, only a few individual animals are encountered in this zone.

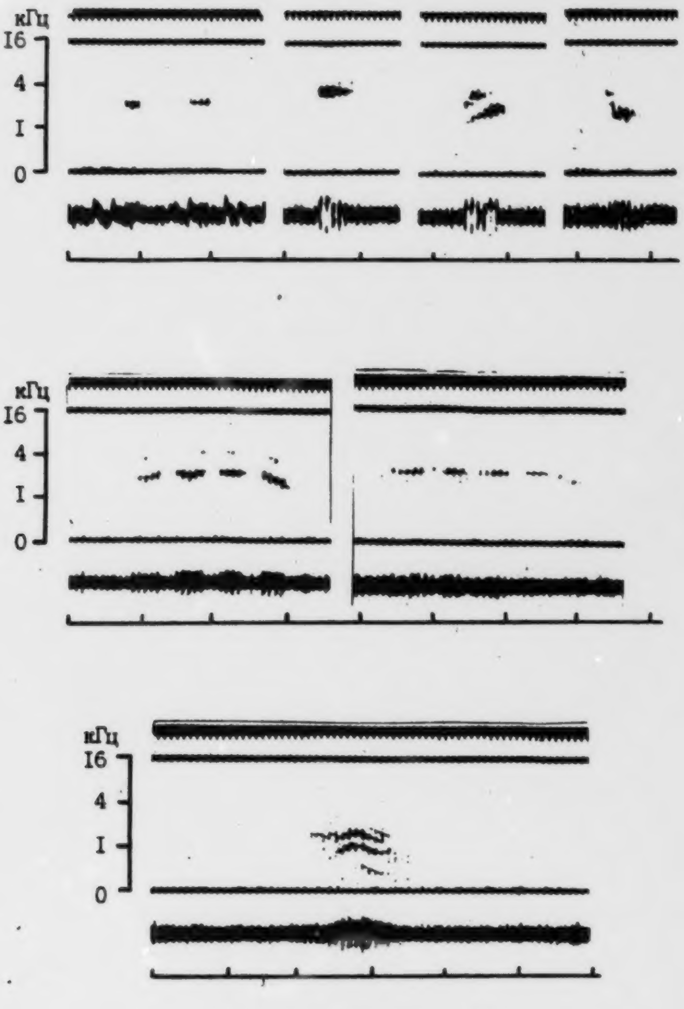
In zone B (sparse low hummocks) the average value of the signals per minute index is equal to 1.4 ± 0.11 (Table 34). The intensity of the signals of the ringed seal for this zone comprises, on average, 1.0 ± 0.09, while the average maximal recorded number of the ringed seal within the radius of the effective operation of the hydrophone in zone B was equal to 1.3 ± 0.13.

In zone V (hummock fields) the average value of the signals per minute index is equal to 5.2 ± 0.66 (Table 35). The intensity of the signals of the ringed seal for this zone comprises 2.5 ± 0.12, on average. The average maximal number of animals, recorded within the radius of the effective operation of the hydrophone, in zone V is 2.7 ± 0.19. Thus, the greatest numbers of ringed seals were found in zone V (fields of hummocks, up to 1.5 m in height).

Table 32

Some frequency-temporal characteristics of the principal classes of signals of the ringed seal (March–April 1984)

Class of signals	Duration of signals (s)	Dominant frequency (kHz)	Number of spectrally analyzed signals; percentage of signals of the given class out of the total number of signals (2918); name of class, comments
No. 1	0.02–0.25	1.1–6.2	95; 39.4%; "Short signals (Figure 27). The signals of this class are very diverse in their characteristics and to the ear they are perceived as "t'yu", "io", "i", etc. They may be combined into series (2–6 signals) with pauses of 0.01–0.35 s. The major part of the energy of the signals falls within the following frequency intervals: 1.1–2.2 kHz (64.3% of the number of analyzed signals); 2–2.4 kHz (10.2%); 2.6–3.2 kHz (10.2%); 3.1–3.8 kHz (8.2%); 3.8–4.6 kHz (4.1%); 5.6–6.2 kHz (3.0%). As the signal proceeds the dominant frequency may remain unchanged, or it may increase by 0.1–0.5 kHz or it may decrease by 0.2–4.4 kHz. Short signals, resembling low frequency barking, with a duration of 0.22–0.25 s have several bands with the major part of the energy: 0.3–0.5 kHz; 0.6–1.0 kHz; 1.0–1.5 kHz (Figure 27V).
No. 2	0.33–1.72	1.0–5.6	109; 36.4%; "Squeal" (Figure 28). The major part of the energy of the majority of the signals is concentrated in the 1.0–2.0 kHz frequency band (62.7% of the number of analyzed signals). A smaller number of signals has other values of the dominant frequencies: 2.6–4.2 kHz (11.8%); 1.6–2.2 kHz (10.9%); 1.0–2.6 kHz (9.1%); 2.0–3.5 kHz (4.6%); 4.6–5.6 kHz (0.9%). Over the course of the signals the dominant frequency may remain unchanged, or increase by 0.2–2.4 kHz, smoothly as the signal proceeds or more abruptly in its final part; or it may decrease by 0.2–1.5 kHz over the course of the whole signal or in its final part over the course of 0.025–0.21 s. Signals of this class may be produced singly or in series.
No. 3	0.25–0.82	2.4–3.8	17; 10.7%; "Tonal signals" (Figure 29 A, B). The major part of the energy is concentrated in the 2.4–2.9 kHz and 3.2–3.8 kHz intervals. The dominant frequency remains unchanged as the signal proceeds or decreases very slightly over the course of the whole signal by 0.2–0.3 kHz.
No. 4	0.72–1.23	0.9–3.2	3; 9.9%; "Chirp" (Figure 29 V). Initial frequency of signal 1.8–2.2 kHz. As the signal proceeds the dominant frequency attains its highest values (3.0–3.2 kHz), after which it decreases smoothly. Final frequency of signals 0.9–1.5 kHz.
No. 5			5; 3.6%; the rest (Figure 30 A, B, V).

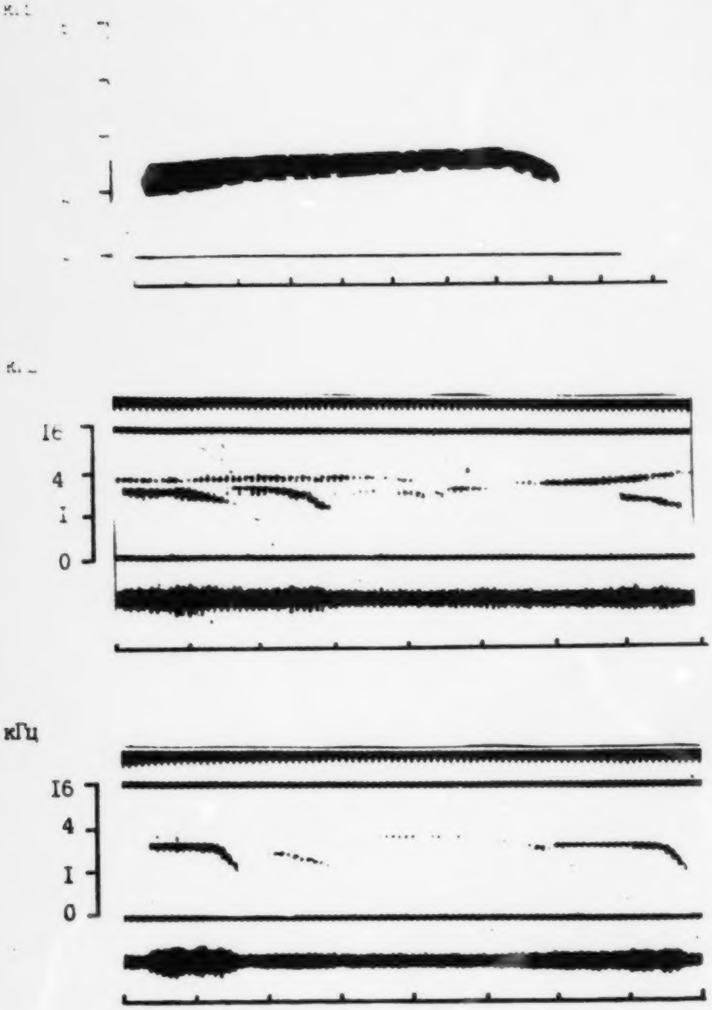


Время: I деление - 0,2 с

Рис.27.Звуковые сигналы кольчатой нерпы класса № I.

Figure 27. Sound signals of class No. 1 of the ringed seal.

ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s



Время: I деление - 0,2 с

Рис. 28. Звуковые сигналы кольчатой нерпы класса № 2

Figure 28. Sound signals of class No. 2 of the ringed seal .

ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

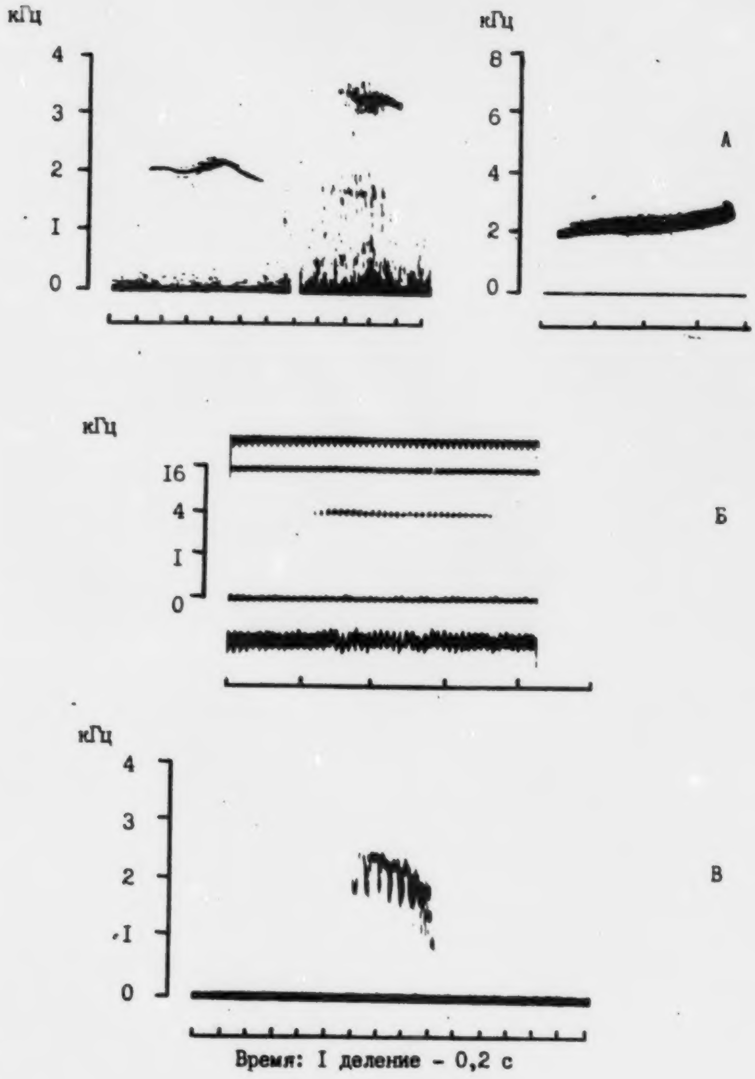
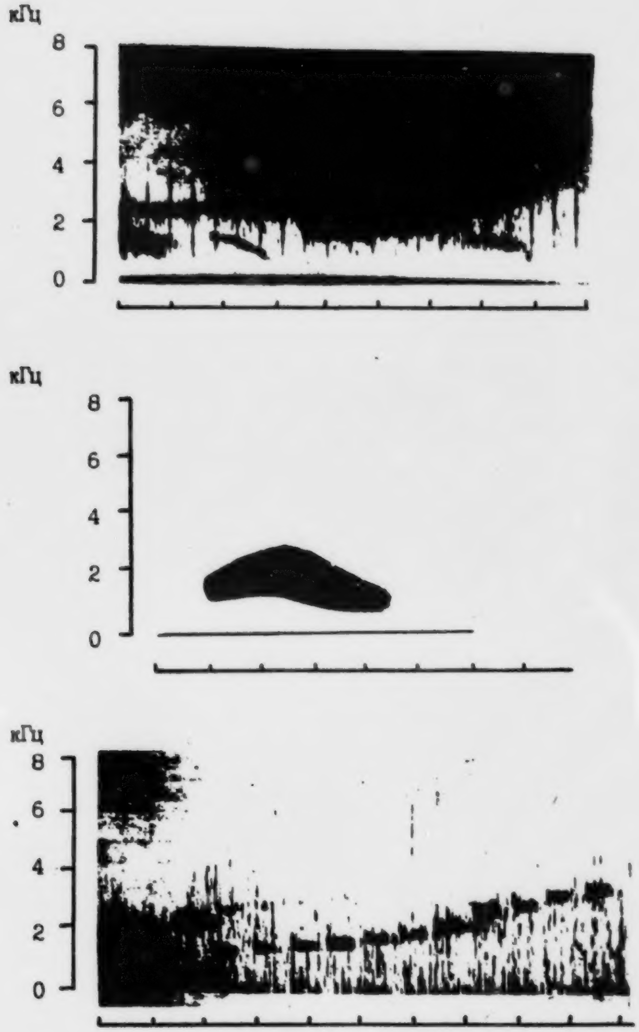


Рис. 29. Звуковые сигналы кольчатой нерпы основных классов: А,Б – № 3; В – № 4

Figure 29. Principal classes of sound signals of the ringed seal.
A, B — No. 3; V — No. 4.

ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s



Время: I деление – 0,2 с

Рис. 30. Звуковые сигналы кольчатой нерпы класса № 5

Figure 30. Sound signals of class No. 5 of the ringed seal .

ordinate: кГц - kHz
abscissa: Time: 1 division - 0.2 s

Table 33.

Characteristics of the acoustical activity and numbers of the ringed seal in zone A (March–April, 1984)

No. of measurement point	0	1	5	6	7	8	9	11	17	22	41	42
Average index of signals / minute	0	0.9	0.5	0.5	0	0	0	0.1	0.8	3.9	0.3	0
Average intensity of signals	0	0.8	0.8	0.8	0	0	0	0	0.5	1.5	0	0
Maximal numbers	0	1	1	1	0	0	0	0		2	0	0
Number of measurements (15 minutes)	1	11	1	1	1	1	1	5	1	1	1	1

Apparently the overwhelming majority of the signals that were recorded at this time belong to sexually mature animals, since it is known that during the pupping and the mating period the greatest density of the adult individuals is found on the stable fast ice, while the non-reproducing individuals are encountered in the zone of the moving ice (J. A. McLaren, 1958; J. J. Burns, 1970; T. G. Smith, 1973).

Daily activity. As a result of the measurements there was found an increase in the level of the acoustical activity of the ringed seal during the morning and the evening hours. Data on the level of the sound activity of the ringed seal in zone V (hummock fields) at different times of day are presented in Figure 31. The average value of the signals/minute index in the interval between 07.00 and 12.00 hours comprised 6.5 ± 1.11, in the 12.00–16.00 hr interval — 3.3 ± 0.36, and in the 16.00–19.00 hr — 5.4 ± 1.01. The analysis showed a significance of the differences of the data in these time intervals.

The higher level (by a factor of 1.9) of the signalization of the ringed seal during the evening hours in comparison with the daytime hours is indicated also by the measurements carried out over the course of one day at particular points in zone V (point 23, 13.00–14.00 hrs — 5.1 signals/minute; 18.00–19.00 hrs — 8.1 signals/minute; point 43, 14.00–15.00 hrs — 5.7 signals/minute; 18.00–19.00 hrs — 10.9 signals/minute).

Table 34.

Characteristics of the acoustical activity and numbers of the ringed seal in zone B (March–April, 1984)

No. of measurement point	Average index of signals / minute	Average intensity of signals	Maximal number	Number of measurements (15 minutes)
2	1.2	1.2	2	15
3	2.4	1.2	2	3
4	1.5	1.0	1	2
10	1.2	1.3	1	5
12	1.0	1.0	1	7
13	3.7	1.5	3	9
14	0	0	0	2
15	1.3	0.6	2	4
16	0	0	0	1
18	1.5	1.5	2	4
19	2.7	1.5	2	3
20	1.5	1.3	1	6
21	1.6	1.0	1	1
27	0.2	0.5	1	1
28	1.3	1.0	1	1
29	1.9	1.3	2	1
34	0.4	1.5	1	1
40	1.9	1.0	1	1
44	2.2	1.0	2	1
45	3.0	1.0	2	1
46	0.9	0.5	1	1
47	1.7	1.0	1	1
48	0.6	0.5	1	1
49	0.5	0.5	1	1
50	2.1	1.8	2	1
55	0.9	1.0	1	1
56	0.9	1.0	1	1
57	0	0	0	1
58	0.8	1.0	1	1

On the whole, however, the acoustical signalization of the ringed seal is characterized by having an extremely inconstant level (Figure 31). The coefficient of variation of the signals / minute indices is equal to 10.4% (data for zone V). An irregular character of the signalization is noted also in some individual points (Figure 32, measurements over the course of 15 minutes at point 43).

The data of the 1987 season on the intensity of the signals and the numbers of the ringed seal in zones A and B (Figure 25) are presented in Table 36. By and large they corroborate the principal conclusion from the data of the 1984 season; the greatest

Table 35.

Characteristics of the acoustical activity and numbers of the ringed seal in zone V (March–April, 1984)

No. of measurement point	Average index of signals / minute	Average intensity of signals	Maximal number	Number of measurements (15 minutes)
23	5.9	2.8	3	13
24	6.6	2.8	3	1
25	3.8	2.3	3	2
26	1.1	1.7	3	17
30	3.0	1.8	2	1
31	4.3	2.0	3	1
32	2.1	2.3	1	1
33	0.8	2.0	1	1
35	6.6	3.0	3	4
36	4.0	3.0	3	2
37	4.1	3.0	3	2
38	4.8	2.5	3	1
39	3.7	1.5	2	1
43	7.9	2.8	4	9
51	6.3	2.5	3	1
52	11.9	2.5	4	1
53	9.3	3.0	3	1
54	7.9	3.5	3	1

number of seals was noted in zone V (fields of hummocks, up to 1.5 m in height, providing for the accumulation of a snow cover of more than 50 cm).

c. Sound signalization during the summer months

During the summertime in July–August of 1986 studies were carried out on the sound activity of the ringed seal in an area of water (Letnyaya Zolotitsa) situated 30 km from the location of the winter investigations in Konyukhovaya Bay. As compared with March–April, the overall level of the acoustical activity of the ringed seal during the summer was considerably lower, by a factor of 7.4, and on average comprised 0.46 signals per minute, with the maximum of the signalization occurring in the evening hours (in the 09.00–17.00 hr interval the signal/minute index comprises 0.3; 17.00–21.00 hr — 4.9; 21.00–01.00 hr — 1.7). Only the time of the tape recording (67 hours) was included in the calculation; if all of the time of the audio-monitoring had been taken into

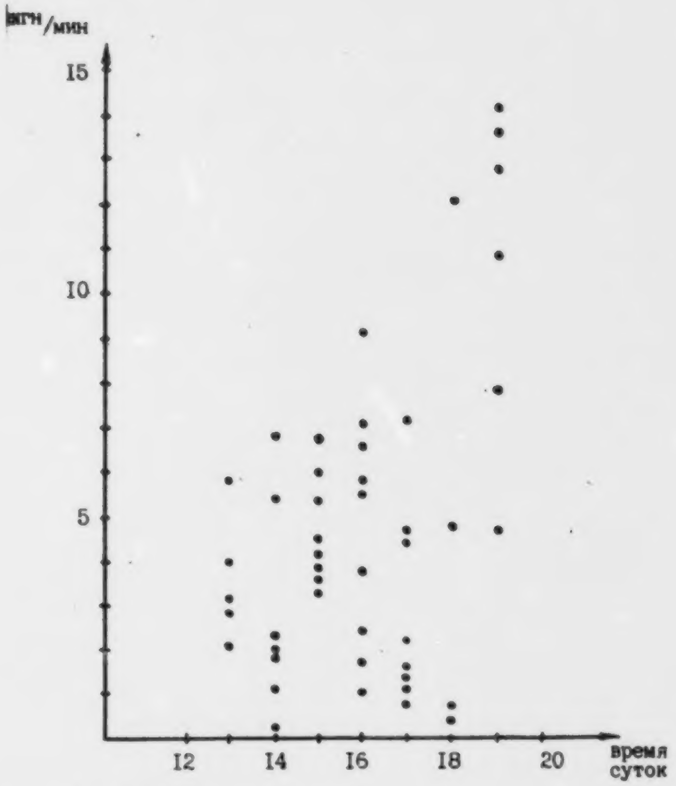


Рис.3I.Динамика уровня акустической активности кольчатой нерпы в различное время суток (данные по зоне В,март-апрель I984 г.)

Figure 31. Dynamics of the level of acoustical activity of the ringed seal at different times of day (data for zone V, March–April, 1984).

ordinate	сигн / мин	- signals / minute
abscissa	время суток	- time of day

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consideration, the values of the index would have been considerably lower. By and large the signalization during the summer months differs somewhat from the winter-spring signalization (Table 32); the proportion of the No. 3 class signals increases (28.2%) and considerably fewer of the No. 4 class signals (2.4%) are recorded.

Audio-monitoring of the area of water during the summer period (August 10–20, 1986) in the immediate vicinity of the mixed rookery of the bearded and ringed seals on the small islands in the region of the winter investigations (Konyukhovaya Bay) showed

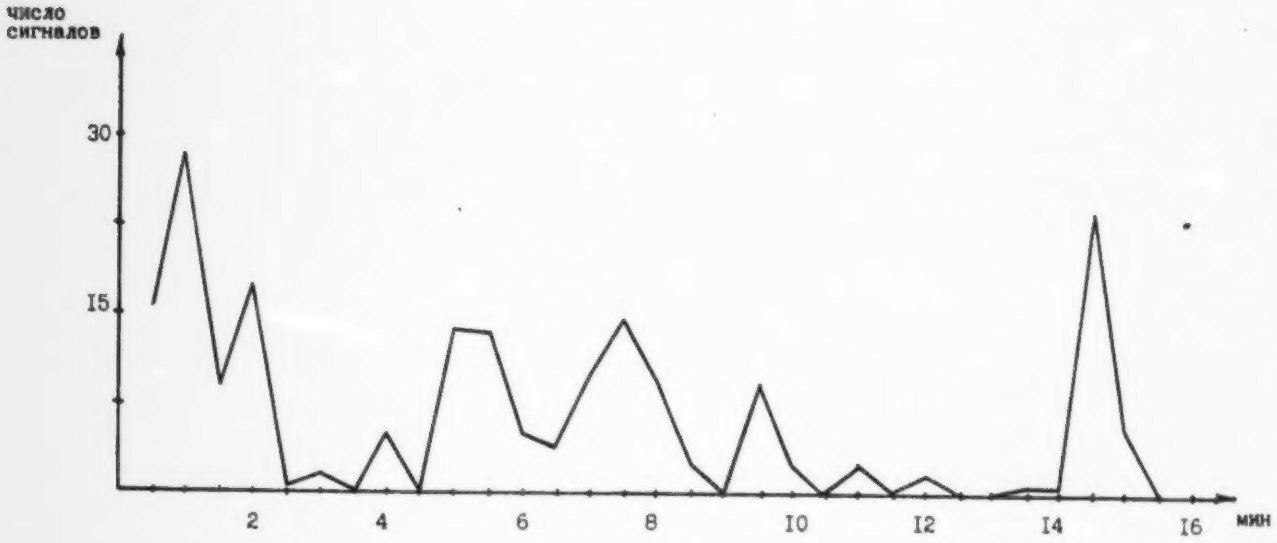

Рис.32.Динамика уровня звуковой сигнализации кольчатой нерпы (т. 43, зона В).

Figure 24. Dynamics of the level of sound signalization of the bearded seal (point 43, zone V).

ordinate	число сигналов - number of signals
abscissa	мин - minutes

Table 36.

Characteristics of the signal intensity and estimation of the numbers of the ringed seal in zones A and V (March–April, 1987)

No. of measurement point	Zone A								Zone V								
	1	3	4	5	6	10	11	12	2	7	8	9	13	15	16	17	18
Average intensity of signals	3.0	0	0	0	0	0	0	0	3.5	0	0	0	3.5	3.0	0	2.0	3.0
Maximal recorded number	2	0	0	0	0	0	0	0	3	0	0	0	3	3	0	1	1
Number of measurements (15 minutes)	2.7	6.4	2.1	2.1	2.1	4.3	2.1	2.1	11.9	2.1	6.4	4.3	2.1	2.1	2.1	4.1	1.2

an absence of signals of the ringed seal (total time of monitoring – 28 hrs). The maximal number of seals noted on the hauling-out grounds was 51. The seals on the small island were scattered in a dispersed distribution, at a distance of 5–15 m from one another.

Thus, the discriminative attitude of the ringed seal to particular kinds and forms of ice in the selection of a region for pupping (stability of fast ice, presence of hummocks up to 1.5 m in height, providing for an accumulation of the snow cover of more than 50 cm in thickness), shown in the studies on the White Sea (L. P. Lukin and V. A. Potelov, 1978) and in Canada (M. O. Hammill and T. G. Smith, 1989), are corroborated by the data of the acoustical method. The highest numbers of seals are noted in the zone that is the most favourable for reproduction — in zone V (fields of hummocks up to 1.5 m in height) (Tables 33–36).

As we have already mentioned, the signals of the ringed seal are produced at all times of the year and, apparently, they are not specifically associated with the reproductive behaviour (I. Stirling, 1973). This author considers as more probable their association with aggressive and subordinative behaviour. In the opinion of I. Stirling et al. (1983) the vocalizations of the ringed seal play an important role in the organization of the social behaviour during the period of reproduction, as occurs in the ecological twin of this species, Weddell's seal (G. W. Kaufman et al., 1975; I. Stirling, 1977). This may explain the 2–13-fold increase in the sound activity which they noted in their data at the end of April, in comparison with other months.

The data obtained by us also provide evidence of an increase in the level of signalization during the period of reproduction, in March–April, by a factor of 7.4 times and more as compared with August. However, we conjecture the presence in the ringed seal of two groups of signals: the first, which are utilized in aggressive and subordinative behaviour, and the second, which are predominantly associated with reproductive behaviour; for example, the percentage of the class No. 4 signals is 4.1 times higher during the period of reproduction as compared with the summer. In order to corroborate this thesis it is necessary to establish a more detailed classification.

It has been noted that the behaviour of the ringed seal is quite often characterized by highly aggressive behaviour. K. J. Finley (1979) observed a male in possession of four dens which he was defending against other males, while two neighbouring dens were occupied by a female with young. According to observations in the region of the Gulf of Riga, a male that was lying near a female drove away an approaching rival, biting it on the flippers, i.e. he forced out the newcomer from the female's sector (M. Leis, 1960). Investigators have also found frozen seals with traces of bites (T. G. Smith and J. Memogana, 1977). During the reproductive period high aggressivity of ringed seal males and females has been noted with respect to other species of seals and also a high degree of conservatism with regard to their own place on the ice (T. G. Smith and M. O. Hammill, 1981).

The utilization of some of the signals in agonistic behaviour is indicated by the overall irregular character of the signalization, by the high value of the coefficient of variation, and by the spasmodic change in the level of acoustical activity at particular measurement points during the winter (Figure 29). The lowering of the level of sound activity during the summer months is in all probability associated with the less dense distribution of the animals in the area of water, with the decrease in the number of social contacts of the animals and with the discontinuance of the signalization specifically associated with reproductive behaviour.

Our data on the daily dynamics of the sound activity of the ringed seals during the period of their life spent under the ice is in agreement, on the whole, with the data obtained by American investigators (W. Calvert and J. Stirling, 1985). These authors noted a high level of signalization in the first half of the day (7–19 signals/minute) and a lower level at night (7 signals/minute).

The question of the estimation of the numbers of the pagophilic species of seals is becoming especially pertinent at the present time in connection with the increasing anthropogenic effect on populations of pinnipeds. The existing methods (counts from aeroplanes and searching for dens with the help of dogs) are very imperfect. Thus the accuracy of aerial counts is low because of the considerable effect of weather conditions on the character of the behaviour of the seals. "Searching for dens" is a laborious method and well trained dogs are required for this.

At the same time many biologists have noted the possibility of the use of recordings of underwater vocalizations for estimating the numbers and distribution of marine mammals (C. Ray, 1970; H. E. Winn et al., 1975; T. G. Smith and J. Stirling, 1978; J. A. Thomas and D. P. Demaster, 1982). An attempt was undertaken to study the underwater vocalizations of the ringed seal and of the bearded seal (J. Stirling et al., 1983). These authors, however, noted some deficiencies in the work that was carried out, consisting of the low quality of the recordings and the poor tie in to the ice conditions.

Our ideas concerning the further development of the acoustical method for estimating the numbers and distribution of marine mammals, with consideration given to the information presented previously (J. Stirling et al., 1983), are as follows: 1) elucidation of the seasonal and daily changes in vocalization for determining the optimal time of recording; 2) the establishment of a classification and catalogues of the signal repertoires of the species; 3) the determination of the time interval for recording, which would most fully reflect the characteristics of the acoustical activity of the species; 4) the revelation of the age, sex and social status of the animals producing the sounds, and 5) the determination of the radius of the effective operation of the hydrophone for the signals of different species .

The behaviour and underwater acoustical activity of the three species of true seals (conclusion)

a. Sound signals and behaviour of the spotted seal, bearded seal and ringed seal.

The data obtained on the acoustical activity and behaviour of the three studied species of true seals indicate significant differences in the frequency-temporal characteristics of the signals, their functional meaning and the character of their utilization.

In the spotted seal the overwhelming majority of the signals are pulsed signals, the dominant frequency of which does not exceed 2.5 kHz, while the duration of series and pulses does not exceed 3 s. The frequency-temporal characteristics of the signals of the Kamchatka and Amur spotted seals are very similar.

Among the signals of the ringed seal there is a predominance of tonal and continuous signals and of signals with a complex structure (pulsed-tonal). Their dominant frequency is higher (0.9–6.2 kHz). The longest signal in the ringed seal is about 2 s.

Finally, all of the signals of the bearded seal comprise whistle-like, frequency- and amplitude-modulated, continuous signals, the dominant frequency of which changes within the limits of 0.3–6.8 kHz. These are the most prolonged signals (0.7–78 s).

In contrast to the White Sea seals, the sound signalization of the spotted seal plays an important role in the organization of its searching and hunting activity. This determines the more diversely structured system of signalization, as compared with the bearded seal and the ringed seal. The individual searching and hunting behaviour of the Kamchatka spotted seal in the river is characterized by waiting tactics (Figure 10); the seal in ambush lies in wait for its prey and selects the moment for the pursuit. The Amur spotted seal also waits for a suitable moment to initiate the pursuit of its prey, periodically moving slowly under the water, close to the surface, above the fish that are moving through the channel. Out of the three species of true seals, echolocation probably occurs only in the spotted seal. We have established, however, that during the pursuit of its prey the spotted seal does not navigate but rather makes use of sonar direction finding. The single and double pulses, or detection and ranging signals, which comprise more than half of all of the signalization, are apparently utilized by the spotted seal for orientation, for finding social partners and for the distant detection of fish during the searching stage.

The group spurts of the Kamchatka spotted seal in pursuit of fish markedly increase the probability of catching the fish, but the behaviour of the animals in this case is entirely based on competitive relationships. The aggressive encounters, which arise in the conflict of the animals over fish, in the defense of a sector of the area of water, that is favourable for hunting, or to clear up the hierarchical status of the seals, are accompanied by communicative and emotional signals (Table 24); and in this case a particular sequence of behavioural elements corresponds to every such sequence of signals.

It is quite probable that in the sea the social interactions of the spotted seal become rarer, as a consequence of the remoteness of the partners from one another. This is corroborated by recordings made by us in a section of an area of water in the sea in the region of the trap net (400 m from the shore and about 5 km from the river). Almost 77% of all of the signals here comprised echolocation signals — single and double pulses (classes No. 1 and No. 2).

As we have already mentioned, the sonar monitoring of the area of water in the region of the observations in the White Sea during the summer and autumn months (more than 1600 hours) indicates a discontinuance of signalization in the bearded seal (121 fragments of signals) and a decrease in its level, to less than one tenth, in the ringed seal. This is associated, in our opinion, with the lesser density of the distribution and with the drastic weakening of the social interactions of the animals. Thus, for the White Sea seals one may speak only of much simpler, in contrast to the spotted seal, solitary forms of hunting, in the organization of which the role of sound signals is very small.

Most of the acoustic signals of the ringed seal are also associated with aggressive and subordinative, and with territorial behaviour. Our data on the character of the signalization of this species are in good agreement with the data of other investigators (J. Stirling, 1973; J. Stirling et al., 1983). At the same time one should not deny the presence in the ringed seal of signals that are predominantly used during the reproductive period (signals of class No. 4).

Having the simplest stereotypic structure, specifically associated only with reproductive and territorial behaviour, is the signalization of the bearded seal.

b. Some features of the social organization of the true seals.

The prolonged evolution of the true seals in the aquatic medium (L. G. Barnes et al., 1985) has determined the development of a whole series of highly perfected morphological and physiological adaptations. The form of the body and of the integument of the animals has changed; most of the organ systems have been affected, especially the respiratory, circulatory, cardiovascular and other systems. An analysis of these changes indicates that, like the toothed whales, the seals are highly specialized aquatic mammals (V. P. Galantsev, 1977). The animals of these groups are for the most part active predators and may stay under water for 60 minutes and more (R. Elsher and D. Hammond, 1969), and they may dive to depths of as much as 900 m (R. J. Harrison, 1960; B. J. Le Boeuf et al., 1988). At the same time the overall level of the social organization of the true seals is substantially less developed than the plastic and complex forms of behaviour that have been noted in associations of the toothed whales (N. A. Krushinskaya and T. Yu. Lisitsyna, 1983; V. M. Bel'kovich and M. N. Shchekotov, 1990; J. F. Allen, 1977; V. S. Gurevich, 1977; J. S. Leatherwood, 1977; B. Würsig and W. Würsig, 1980; K. S. Norris et al., 1982; S. M. Johnson and K. S. Norris, 1986, and others).

The three species of seals that were examined — the spotted seal, the bearded seal and the ringed seal — form only temporary aggregations in places that are suitable for their reproduction, moulting and intensified feeding; the interrelationship of the individuals within these aggregations is not clearly expressed, it is irregular and unstable. During the main part of the herring run, which takes place in the coastal zone of the sea, the spotted seals aggregate mainly beside the capes, in the marine currents (S. Yu. Freiman, 1936). In the summer and in the autumn the spotted seals become concentrated in large numbers (up to 2–3 thousand animals) in the estuarine expanses of rivers, which is associated with the mass spawning runs of salmonids. Along with the large aggregations, the spotted seal forms small groups (10–50 individuals) in places with particular favourable conditions for the pursuit and capture of fish (topography of the bottom, etc.). The interaction of the seals in this case is limited only to aggressive-competitive relations. The on-shore rookeries of this species, which appear predominantly at night and during low tide, are also unstable and all of the intercourse of the animals in them may be limited to weakly expressed aggressive encounters as they move across the hauling-out grounds. The rookeries of the spotted seal are dense, with the distance between individuals not exceeding 40–50 cm. The moulting rookeries may apparently be more differentiated in sex and age, since the sexually immature individuals moult first, the males are next and the adult females are last in turn (S. P. Naumov, 1941; G. A. Fedoseev, 1965; G. M. Kosygin and V. N. Gol'tsev, 1971; G. G. Shmakova, 1978; L. Thompson and P. Rothery, 1987). This conjecture is corroborated also by the seal hunt data (G. G. Bobrova, 1982).

A comparatively high density of the White Sea seals — of the bearded and ringed seals — is found only in the winter during the reproductive period in the region of the fast ice, and in this case the greatest numbers and highest level of acoustical activity of the seals is found in the zone of densely situated hummocks, where the accumulation of a snow cover is ensured, which is necessary for the construction of pupping dens. The studies on the fast ice, carried out jointly with the Northern Polar Scientific Research Institute of Marine Fisheries and Oceanography (Arkhangel'sk), using the traditional method of searching for holes and dens with dogs and also the acoustical method, showed a correspondence of the data obtained by these methods (Table 31).

The audio-monitoring of the areas of water during the summer and autumn months (more than 1600 hours) indicates an almost complete discontinuance of signalization in the bearded seal and a decrease in its level, to less than one tenth, in the ringed seal. In our opinion, this is associated with the lesser density of the distribution and with the drastic weakening of the social interactions of the animals. Visual observations at this time showed that individuals of both species occupy sectors of the area of water near the shore, with a diameter of 1–2 km. The on-shore rookeries of these species are also greatly dispersed: the distance between resting seals in the case of the ringed seal comprised 5–15 m, and of the bearded seal — 10–20 m. The rookeries of the "lakhtak" [the Pacific subspecies of the bearded seal] on the ice are characterized by the seals being at some considerable distance from one another, and in the case when they are found on one ice floe the animals are oriented in different directions (S. S. Lun', 1936; J. J. Burns, 1981).

The period of the care of the progeny in the three studied species of true seals is not prolonged and practically coincides with the time of lactation: about a month in the spotted seal, about a month and a half in the ringed seal and in the bearded seal it is very short — about two weeks.

Characteristic of the spotted seal is the formation (at the time of reproduction) of constant pairs, which remain together over the course of the entire nursing period (E. A. Tikhomirov and G. M. Kosygin, 1966; E. A. Tikhomirov, 1969). In the males of the spotted seal the period of their distribution on the family territories proceeds without any substantial aggressive encounters, judging by the fact that usually no scars nor wounds are found on the skin (K. K. Chapskii, 1976). The "family" groups, consisting of a lactating female, of its young and of the male, hold themselves in a dispersed fashion, rarely closer than 200-300 m from one another (F. H. Fay, 1974), and the adult individuals may defend their territory against the intrusion of other animals (M. A. Bigg, 1981). The lactation continues for about a month and, as in the White Sea seals, apparently only the mother takes care of the young.

Mating is preceded by a period of courting (of about two weeks) during which the male pursues the female, biting her on the neck and clasping her with his fore flippers (according to observations in captivity, J. C. Beier and D. Wartzok, 1979). All of this is accompanied by a large number of acoustic signals, such as growling, long series of pulses, snorting and squeaking. Copulation occurs under water. The pre-copulatory behaviour included naso-nasal contacts, paired synchronous and spiral swimming, biting of the neck, inflating the neck, swelling of the body and clapping of the jaws. Similar nuptial behaviour in the natural habitat conditions have been noted also in the closely related common seal (H. M. Venables and L. S. Venables, 1955, 1957, 1959; R. M. Sullivan, 1981; S. G. Allen, 1985).

The young of the ringed seal are born over a period of one to one and a half months from the middle of March to the middle of April (K. K. Chapskii, 1940; M. Nishiwaki, 1972). Characteristic of this species is the construction of the special snow dens during the period of the appearance and feeding of the progeny (T. G. Smith and J. Stirling, 1975; L. P. Lukin and V. A. Potelov, 1978; L. P. Lukin, 1975). Several types of dens have been noted: male dens, dens for a female with young, "infant" dens and complexes of these (T. G. Smith and J. Stirling, 1975). The behaviour during the construction of the snow den is characterized by a fairly high degree of complexity (N. L. Krushinskaya and T. Yu. Lisitsyna, 1983). In the ringed seal in the Sea of Okhotsk the birth may occur also on open ice floes, not under a snow cover (G. A. Fedoseev, 1964, 1965).

Lactation continues for about a month and a half (K. J. Frost and L. F. Lowry, 1981) and in the course of this the females of the ringed seal display care of their young, attempting to aid the pup in case of danger and even defending it (P. Perri, 1974).

During the second half of the nursing period the number of contacts of the sexually mature females and males of the ringed seal increases in connection with the beginning of the rut. Quite a few investigators have noted a high aggressivity of the ringed seal and territoriality, in connection with which it has been conjectured that this species is monogamous (M. Leis, 1960; T. G. Smith and J. Memogana, 1977; J. Stirling, 1977).

Lactation in the bearded seal lasts for a comparatively short time, 12–18 days, and moreover at the end of this period the pup commences to feed independently and actively continues feeding after the termination of nursing, in contrast to the young of the ringed seal and of the spotted seal, which do not start to feed immediately but consume the fat that accumulated during the period of nursing (J. J. Burns, 1981). The newly born young are immediately able to swim and dive (V. I. Krylov et al., 1964).

The bond of the females with the young is especially strong at the start of the nursing period, which is manifested in the attempts of the female to protect and assist the young when taking flight (É. A. Tikhomirov, 1964).

The period of reproduction in the bearded seal coincides with the termination of lactation (V. A. Potelov, 1975). The nuptial behaviour of the bearded seal is manifested by the excited state of the animals, by their pursuing one another, and at this time a high level of the sound activity of the animals is found (A. N. Dubrovskii, 1937). There is an interesting report on the formation of pairs in bearded seals in the last days of August (L. G. Rutilovskii, 1939).

On the whole, however, it may be said that the fundamental care of the mother for the young in the spotted seal, bearded seal and ringed seal consists of the intensive feeding of the newly born pups with milk; the young of the true seals proceed along the major part of the pathway of their ontogenetic development without contact with their mother (Yu. K. Timoshenko, 1978; N. L. Krushinskaya and T. Yu. Lisitsyna, 1983; V. S. Nikulin, 1986; K. M. Kovach, 1987, and others). The young possess a set of innate and determined forms of behaviour, which give to them the ability to survive during their transition to an independent way of life (O. A. Rasa, 1971). During the play of the young animals the development of their coordination proceeds, as does also the physical and mental development of the young animals (N. P. Zimenko and V. M. Smirin, 1986; R. L. Gentry, 1974). The young spotted seals spend a considerable part of their time in play in the water and on the on-shore "juvenile" rookeries, which are set apart from the adult rookeries. The attitude of the adult individuals to the young true seals is either indifferent or aggressive

(Z. Ober de la Ryu, 1957; J. C. Coulson and G. Hickling, 1964; L. A. Popov, 1966; S. C. Fogden, 1971; R. W. Burton et al., 1975). We have observed similar behaviour, in most cases weakly aggressive, in the attitude of adult spotted seals to the young seals on the on-shore rookeries.

Sounds play a large role in maintaining the contact of the mother and young during the nursing period in the true seals (L. A. Popov, 1967; R. Warham, 1964; H. T. Andersen, 1969; L. Petrihovich, 1974; A. Cornet and P. Jouventin, 1980). The calling cries of the young are not infrequently propagated both through the air and under water (J. W. Lawson and D. Renouf, 1987). However, with the transition of the young animal to an independent way of life this bond is apparently completely broken-off, being continued for some time only in the Weddell seal (G. W. Kaufman et al., 1955). All of our attempts to record any underwater sounds of the young spotted seals, which at that time were already living independently, did not have a successful ending.

At first glance in the series "bearded seal – ringed seal – spotted seal" there is evident a certain relationship (Table 37) between the ecological factors of the environment (activity, accessibility and predictability in time and space of the principal food objects) and the structure of the associations, as well as the degree of utilization of sound signalization in the formation and maintenance of this structure, as has been shown and is proposed for many other species of animals (E. O. Kleiman, 1967; J. F. Eisenberg, 1972; K. S. Norris et al., 1972; E. O. Wilson, 1975; P. Marler, 1976; N. B. Davis and J. R. Krebs, 1978). Of interest in connection with this are the data on the feeding of the lakhtak, the ringed seal and the spotted seal in the Sea of Okhotsk and the Bering Sea (Yu. A. Bukhtiyarov, 1986). The average relative share of invertebrates in the food of the seals comprised, respectively, 89.0%, 59.9% and 15.9%. In this case one should take into consideration that out of the listed species of seals only the spotted seal feeds for the most part on cephalopods.

In conclusion it may be said that competitive relations, aggressivity, a brief contact of the mother with its young and an absence of training during the nursing period are

Table 37

Character of the feeding and of the behaviour of the three species of true seals

Species	Principal objects of feeding	Social conditions	Number of principal classes of underwater sound signals, their functional purpose	Level of acoustical activity
1	2	3	4	5
Bearded seal	Crustaceans, gastropod & bivalve mollusks, crabs, holothurians, small schooling fish – Arctic cod, herring; non-schooling fish – flounders, gobies* (1-6)	Relatively high density in the reproductive period, spring-summer distribution scattered, as are the rookeries on the shore and on the ice (7-9, our data)	5; reproductive and territorial behaviour (10-11)	High in reproductive period (March–April), discontinuance of signalization in the summer and autumn months
Ringed seal	Small schooling fish — navaga, cod, crustaceans (12-17)	As for bearded seal (12, 15, 18-21)	5; aggressive and subordinative, possibly reproductive behaviour (11, 22-24)	High at time of reproduction (March-April), decreased level of (to less than one tenth) in the summer and autumn
Spotted seal	Large, rapidly moving objects — various species of salmonids, cephalopods, small schooling fish — Alaska pollock, herring (25-28)	Relatively low density in reproductive period. Considerable aggregations at times of intense feeding and moulting (July-October), very dense and numerous on-shore rookeries (7, 29)	13; aggressive behaviour, organization of searching and hunting behaviour, possibly echolocation, nuptial behaviour (30-32)	High in reproductive period (March–April). High level of signalization during intense feeding (July–October)

1 – Tomilin A. G., 1970; 2 – Kosygin G. M., 1971; 3 – Fedoseev G. A. and Bukhtiyarov Yu. A., 1972; 4 – Stirling I. et al., 1977; 5 – Popov L. A. and Bukhtiyarov Yu. A., 1982; 6 – Finley K. J. and Evans 1983; 7 – Lun' S. S., 1936; 8 – Freiman S. Yu., 1936; 9 – Burns J. J., 1981; 10 – Ray C. et al., 1969; 11 – Shchekotov M. N. and Agafonov A. V., 1988; 12 – McLaren J. A., 1958; 13 – Fedoseev G. A., 1965; 14 – Lowry L. F. et al, 1980; 15 – Frost K. J. and Lowry L. F., 1981; 16 – Bukhtiyarov Yu. A. and Popov V. N., 1982; 17 – Timoshenko Yu. K., 1982; 18 – Burns J. J., 1970; 19 – Burns J. J. and Harbo S. J., 1972; 20 – Smith T. G., 1973; 21 – Stirling I., 1974; 22 – Stirling I., 1973; 23 – Winn H. E. and Schneider J., 1977; 24 – Stirling I. et al., 1983; 25 – Popov L. A. and Bukhtiyarov Yu. A., 1975; 26 – Bukhtiyarov Yu. A., 1978; 27 – Bukhtiyarov Yu. A. et al., 1990; 28 – Burkanov V. N., 1990; 29 – Vyatkin P. S. and Burkanov V. N., 1982; 30 – Beier J. C. and Wartzok D., 1979; 31 – Bel'kovich V. M. et al., 1982; 32 – Bel'kovich V. M. and Shchekotov M. N., 1987.

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* The Russian word "bychki", used here, is used for both gobies (Gobiidae) and sculpins (Cottidae). [Tr.]

characteristic of the three studied species of true seals. The social behaviour of the true seals is expressed unevenly over the course of the year and is manifested seasonally in the temporary concentrations of animals in the places that are suitable for reproduction, moulting and intensified feeding. Studies on various species of mammals have shown that the duration of the close social contact of the young animal with its mother and other individuals, of the social training situation, has an effect on the evolution of the social structure of the species (J. F. Eisenberg, 1981, 1986).

The true seals have preserved their connection with the land — the birthing and nursing of their progeny occurs on land or on the ice. In most cases this imposes stringent requirements regarding the period of the rearing of the young animals. In the true seals this is very brief. Furthermore, as we have already stated, the major part of the care of the mother for the young in most species is limited to the intensive feeding with milk of the new-born animal. The social interactions of the young of the true seals with other members of the association for the most part bear an agonistic character. In our opinion all of this imposes certain limitations on the evolution of the social behaviour of the seals.

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Sounds glossary:

блеяние	bleating
визг	squeal
воркование голубя	dove's cooing
ворчание	growl
жужжание	buzzing
зовущий крик	calling cry
крик чайки	gull's cry
лай	barking
морзянка	Morse code
мычание	mooing
призывные крики	calling cries
пыхтение	puffing
раскатистый рев	booming bellow
рев	howl
ржание	whinnying, whinny
рыкать	to roar
рычание	growling
сверчкобые крики	cricket cries
свист	whistle
скрежет	rasping
скрип	squeak
сопение (угрожающее сопение)	huffing (threatening huff)
стон	moan
трель	trill
турнирный крик	combat cry
тьйок	tiok ?
удар	bang, (crack)
фырканье	snorting
хорканье (угрожающее хорканье)	coughing (threatening cough)
храпение (угрожающее храпение)	snorting (threatening snort)
хрюк	grunt
цоканье	clatter
чавканье	champing [mlaskanie]
чириканье	twittering
шипеть	hiss
щебет	chirp
щелчок	click